

**Systematic studies of oryzomyine rodents
(Muridae: Sigmodontinae): definition and distribution of
Oligoryzomys vegetus (Bangs, 1902)**

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Abstract.—Morphological and distributional evidence is presented to document the specific stature of *Oligoryzomys vegetus* (Bangs, 1902) and to clarify its identification with respect to Central American populations of *O. fulvescens*. The geographic range of *O. vegetus* covers not only the mountains of western Panama but also the cordilleras de Tilarán, Central, and Talamanca of Costa Rica, generally above 1000 meters elevation and within lower montane and montane biotic zones. Within southern Central America, populations of *O. fulvescens* usually occur from sea level to 1000 meters in wet tropical and subtropical associations, but numerous instances of sympatry with *O. vegetus* are recorded in the 1000–1500 meter zone. Two species-group taxa, both described from Costa Rica, are allocated to subjective junior synonymy under *O. vegetus*, namely *Oryzomys fulvescens creper* Goodwin, 1945 and *Oryzomys fulvescens reventazoni* Goodwin, 1945. With improved understanding of its taxonomy and geographic range, *Oligoryzomys vegetus* emerges as another species of small terrestrial mammal restricted to the highlands of Costa Rica and western Panama, a region which has formed a modest center for mammalian endemism in southern Central America.

In 1902, Outram Bangs reported two species of *Oligoryzomys* occurring together at Boquete and its vicinity, on the southeastern slopes of Volcán de Chiriquí between 3800 and 4800 ft in western Panama. Five specimens, ranging in age from young to old adults, were identified as Allen's (1893) *Oryzomys costaricensis*; 13 others, however, about the same in age span, were larger-bodied with darker fur, bigger hindfeet, and longer, monocolored tails. The latter Bangs (1902) described as a new species, *Oryzomys* (*Oligoryzomys*) *vegetus*. To Bangs, the collection of *Oligoryzomys* from Volcán de Chiriquí was clearly separable into two species, and the comparative data he listed support this view.

Two years later, Allen (1904a) examined seven additional specimens from Boquete, collected by J. H. Batty in 1901, and compared them with Bang's original material. Allen (1904a:69) at first did not appreciate the distinctions between the forms Bangs had identified as *costaricensis* and *vegetus*: "The type and 12 topotypes of *O. vegetus*, kindly sent me for examination by Mr. Bangs, do not differ appreciably from the type, 3 topotypes, and additional Costa Rica specimens of *O. costaricensis*. They also agree with the 7 Boquete specimens collected by Mr. Batty, which I unhesitatingly refer to *O. costaricensis*." In a brief commentary on previously described forms of *Oligoryzomys*, Allen later stated (1916:526):

"The Mexican and Central American forms¹ [His footnote listed *fulvescens* Saussure, 1860, *costaricensis* Allen, 1893, *vegetus* Bangs, 1902, and *nicaraguae* Allen, 1910] that have been recognized are probably only geographic races of *O. fulvescens* (Saussure). A reexamination of *vegetus*, of Chiriquí, proves it to be quite easily separable from either *fulvescens* or *costaricensis*." The context of Allen's remarks suggests that he had reappraised *vegetus* and would consider it valid at least as a subspecies, a viewpoint thereafter formalized by Goldman (1918).

Goldman (1918), in his revision of North American *Oryzomys*, concurred with Allen's (1904a) original doubt about the specific separation of *vegetus* from *costaricensis*. Nevertheless, he considered the Boquete form sufficiently distinct to retain it as a subspecies of *Oryzomys fulvescens*, and he did likewise for *costaricensis*. Goldman's formal action considerably expanded the morphological definition of *Oryzomys (Oligoryzomys) fulvescens* to embrace populations distributed geographically from northeastern Mexico, throughout Middle America, to eastern Panama, and ranging altitudinally from near sea level to over 3000 m (Fig. 1). The trinomial recognition of *vegetus* has been subsequently observed both in regional geographic treatments (Goldman 1920, Goodwin 1946, Handley 1966) and in authoritative classifications of North American Mammalia (Miller 1924, Miller & Kellogg 1955, Hall & Kelson 1959, Hall 1981).

The experience and observations of other museum and field workers have cast some doubt on Goldman's (1918) interpretation of the relationship and status of *Oligoryzomys* populations in western Panama. In the Field Museum of Natural History, a penciled note—in the script of Wilfred H. Osgood (fide P. Hershkovitz and B. Patterson), dated 7 November 1932, and found in a tray of Panamanian *Oligoryzomys*—reads: "Goldman makes *vegetus* a subspecies of *fulvescens*, but its larger skull and

longer tail, darker coloration etc. seem to make this doubtful." In the Academy of Natural Sciences, Philadelphia, Robert K. Enders deposited large series of *Oligoryzomys* that he collected from the Chiriquí region of Panama in the 1930s. The extensive erasing and overwriting of identifications (*fulvescens costaricensis* or *f. vegetus*) penciled on the skin tags suggest the confusion Enders encountered in trying to reconcile the variation in his samples with Goldman's taxonomy. For example, at Río Gariche, around 1600 m, Enders identified the two "subspecies" *costaricensis* and *vegetus* as occurring at the same locality (ANSP 18408-9). In like manner, recent samples taken from western Panama have impressed field workers of the morphological distinction and sympatric overlap of *vegetus* and *fulvescens costaricensis* (USNM series from NE San Felix, collected by Ronald H. Pine in June–July, 1980).

Such examples, together with our earlier restudy of the critical series in the Museum of Comparative Zoology, have led us to agree with Bangs's (1902) original assessment of *Oligoryzomys* in western Panama (Carleton & Musser 1989, Musser & Carleton 1993). Bangs presented data from what are clearly samples of two species of *Oligoryzomys*, *O. fulvescens costaricensis* and *O. vegetus*. The purposes of this report are: 1) to consolidate the evidentiary basis for the specific recognition of *O. vegetus* (Bangs, 1902); 2) to more fully document the geographical and altitudinal distribution of *O. vegetus* based on larger samples of museum specimens; and 3) to attribute *Oryzomys fulvescens reventazoni* Goodwin, 1945 and *Oryzomys fulvescens creper* Goodwin, 1945 as subjective junior synonyms of *Oligoryzomys vegetus*.

Materials and Methods

Specimens reported herein consist principally of skins with their associated skulls from the following institutions and muse-



Fig. 1. Central American distribution of *Oryzomys (Oligoryzomys) fulvescens* as set forth by the revision of Edward A. Goldman (1918). Geographic races included (adapted from Hall 1981): 1) *O. f. engraciae* Osgood, 1945; 2) *O. f. fulvescens* (Saussure, 1860); 3) *O. f. lenis* Goldman, 1915; 4) *O. f. pacificus* Hooper, 1952; 5) *O. f. mayensis* Goldman, 1918; 6) *O. f. nicaraguae* Allen, 1910; 7) *O. f. creper* Goodwin, 1945; 8) *O. f. reventazoni* Goodwin, 1945; 9) *O. f. vegetus* Bangs, 1902; 10) *O. f. costaricensis* Allen, 1893.

ums: Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York City (AMNH); Field Museum of Natural History, Chicago (FMNH); Louisiana State University Museum of Zoology, Baton Rouge (LSUMZ), Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of Natural History, University of Kansas, Lawrence (KU); University of Michigan Museum of Zoology, Ann Arbor (UMMZ);

National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Type specimens and original series of *costaricensis* Allen (1893), *creper* Goodwin (1945), *nicaraguae* Allen (1910), *pacificus* Hooper (1952), *reventazoni* Goodwin (1945), and *vegetus* Bangs (1902) were studied firsthand.

Approximately 800 museum specimens of *Oligoryzomys* were examined (see full locality information in Taxonomic Summa-

ry), though only some 550 were measured, of which still smaller geographically cohesive subsets were identified for the various numerical analyses. Relative age was coarsely indexed by degree of molar wear to the four age-classes (juvenile, young-, full-, and old-adult) recognized by Carleton & Musser (1989). Emphasis was placed on accruing samples from Costa Rica and Panama to illuminate the morphological differentiation and distribution of *O. vegetus* and *O. fulvescens costaricensis*, but representatives of certain northern subspecies—namely, *O. f. fulvescens*, *O. f. nicaraguae*, and *O. f. pacificus* (according to range limits as given by Hall 1981)—were included for comparative purposes. These operational taxonomic units (OTUs), their sample sizes, and specific localities are recognized as follows.

Oligoryzomys vegetus

- CR1: $n = 13$, from Costa Rica, Limon, Valle El Silencio.
 CR6: $n = 12$, from Costa Rica, Alajuela, Villa Quesada and Tapesco.
 CR7: $n = 17$, from Costa Rica, Puntarenas, Monteverde.
 PA4: $n = 19$, from Panama, Chiriquí, Boquete (type locality of *vegetus* Bangs, 1902).
 PA5: $n = 35$, from Panama, Chiriquí, localities along the upper valley of the Río Chiriquí Viejo (Boquete Trail, Casa Tilley, Cerro Punta and environs, Finca Martinz).
 PA6: $n = 68$, from Panama, Chiriquí, Siola.
 PA8: $n = 12$, from Panama, Chiriquí, Río Chebo and Cerro Pando.

Oligoryzomys fulvescens costaricensis

- CR2: $n = 24$, from Costa Rica, Puntarenas, Cañas Gordas.
 CR3: $n = 5$, from Costa Rica, Puntarenas, El General (type locality of *costaricensis* Allen, 1893).

- CR4: $n = 25$, from Costa Rica, San José, San Geronimo de Pirrís.
 CR5: $n = 26$, from Costa Rica, Cartago, localities along the upper valley of the Río Reventazón (Cartago, Cervantes, El Muñeco, Santa Teresa Peralta, Turrialba and environs).
 PA1: $n = 16$, from Panama, Panama, Cerro Azul.
 PA2: $n = 19$, from Panama, Cocolé, El Valle and vicinity.
 PA3: $n = 20$, from Panama, Chiriquí, Colorado Camp.
 PA7: $n = 28$, from Panama, Chiriquí, Finca Santa Clara and Río Santa Clara.

Oligoryzomys fulvescens fulvescens

- FUL: $n = 57$, from Mexico, Veracruz, various localities including the restricted type locality (Orizaba) of *fulvescens* (Saussure, 1860).

Oligoryzomys fulvescens nicaraguae

- NI1: $n = 23$, from Nicaragua, northcentral highland localities (following Jones & Engstrom 1986).
 NI2: $n = 7$, from Nicaragua, southwest coastal localities (following Jones & Engstrom 1986).

Oligoryzomys fulvescens pacificus

- PAC: $n = 19$, from Mexico, Chiapas, Ariaga, Maspastepec (type locality of *pacificus* Hooper, 1952), and Piji-japan.

To assist verification of place-names and geographic coordinates used in preparation of the distribution map, we consulted gazetteers and-or maps provided in revisionary and faunal works, principally those in Fairchild & Handley (1966), Goldman (1920), Hooper (1952), McPherson (1985), and Slud (1964).

Three external and 16 skull dimensions

(values in millimeters, mm) were recorded and analyzed to summarize patterns of variation within and between the populations sampled. Total length (TOTL), tail length (TL), and hindfoot length (HFL) are those recorded by a collector on the skin label. Crania were viewed under a dissecting microscope when measuring the 14 cranial and two dental variables to 0.01 mm using handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations as used herein, include (see Fig. 2 for landmarks): occipitonasal length (ONL); zygomatic breadth (ZB); breadth of braincase (BBC); breadth across the exoccipital condyles (BOC); least interorbital breadth (IOB); length of rostrum (LR); postpalatal length (PPL); length of bony palate (BPL); length of upper diastema (LD); length of incisive foramen (LIF); maximum breadth across incisive foramina (BIF); breadth across bony palate (BBP); breadth of zygomatic plate (BZP); coronal length of maxillary toothrow (LM1–3); coronal width of first upper molar (WM1); and length of auditory bulla (LAB). Anatomical terminology follows Carleton & Musser (1989) for general features of the oryzomyine skull.

Univariate and multivariate computations were restricted to specimens assigned to the three adult cohorts (young, full, and old). Standard descriptive statistics (mean, range, standard deviation) were derived for the OTUs. One- and two-way analyses of variance, discriminant functions, and principal component analyses were computed using the three external and 16 craniodental variables, all of which were first transformed to natural logarithms. Principal components were extracted from the variance-covariance matrix, and loadings are expressed as Pearson product-moment correlation coefficients of the components with the original external and cranial variables. All analytic procedures were carried out using Systat (Version 5.0, 1992), a series of statistical routines programmed for microcomputers.

Comparisons of
Oligoryzomys fulvescens costaricensis
(Allen, 1893) and *O. vegetus* (Bangs, 1902)

External and craniodental variation.—In diagnosing *vegetus*, Bangs (1902) drew attention to its longer hindfoot and larger, heavier skull, especially with wider zygomatic span, as compared to examples of *costaricensis* (then recognized as a species). The better sample sizes now available bolster Bangs's impression of their salient contrast in size, with specimens of *vegetus* consistently averaging greater in most univariate comparisons (Appendix). Lengths of tail (TL) and hindfoot (HFL) provide key characters for first-approximation identification in the field, with TL usually exceeding 110 mm in adult *vegetus* (usually <110 mm except in oldest *fulvescens*) and with HFL typically 22 mm or greater in adult *vegetus* (usually ≤ 22 mm in *fulvescens*).

Two constellations of points, which correspond to our independent identification of species, are apparent within the plane of the first two principal components extracted for all intact specimens of *Oligoryzomys* from Costa Rica and Panama (Fig. 3). The first two components together account for 68 percent of the variation in the original variable data (Table 1); whereas, the amount explained for components three through 19 is five percent or less for each, and bivariate plots of these disclose no meaningful discrimination of taxa. The 95% confidence ellipse for scores of *vegetus* on PC I versus PC II contains not only specimens from Panama but also those from many localities in Costa Rica. Moreover, each species ellipse circumscribes many specimens taken at the same collecting locality—such as Boquete, Río Chebo, and Finca Santa Clara in Panama, and El Muñeco and Santa Teresa Peralta in Costa Rica (see Specimens Examined). Although individuals from sympatric localities are not identified in Fig. 3 due to visual congestion, certain specimens that do bear on our taxonomic interpreta-

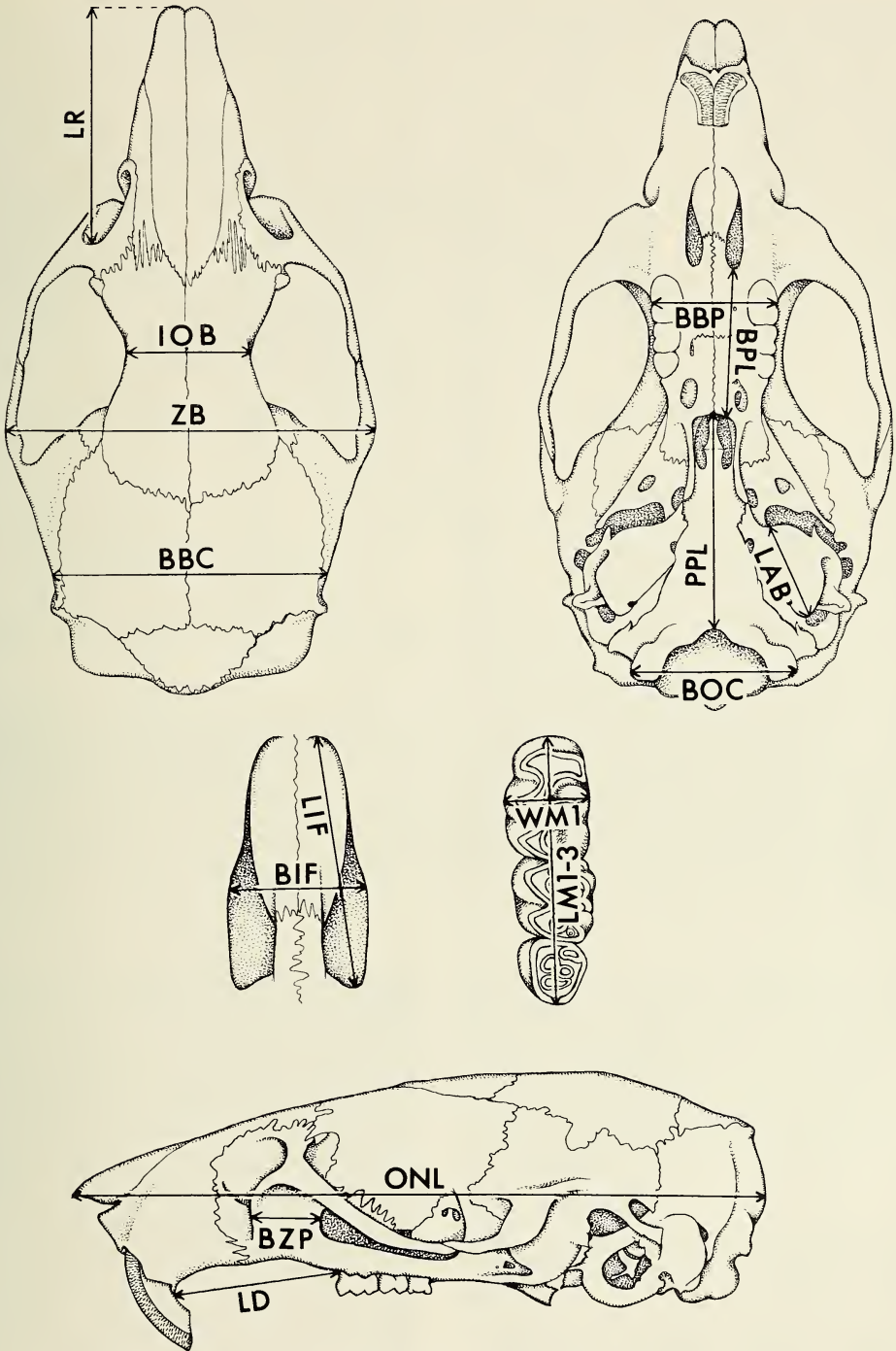


Fig. 2. Schematic views of the cranium (dorsal, ventral, lateral), right maxillary molar row, and incisive foramina of an adult *Oryzomys alfaroi* illustrating the limits of the 16 craniodental measurements recorded for specimens of *Oligoryzomys* (see Materials and Methods for abbreviations).

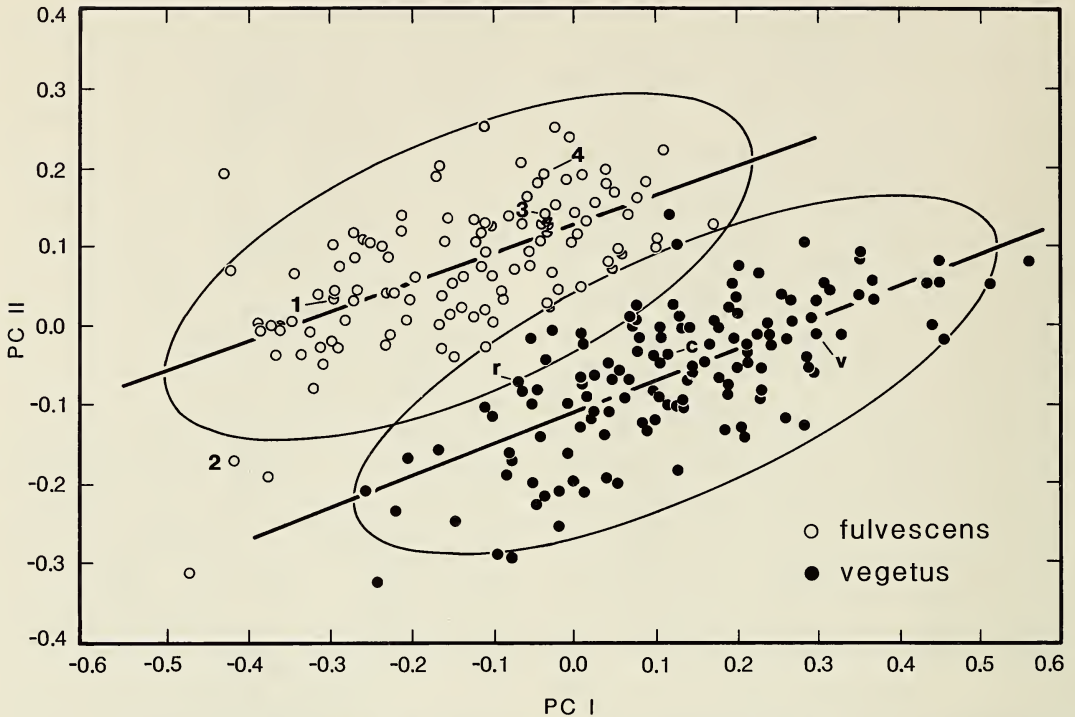


Fig. 3. Projection of individual specimen scores, based on log-transformed external (3) and craniodental (16) variables, onto the first two principal components for samples of *Oligoryzomys fulvescens costaricensis* ($n = 115$) and *O. vegetus* ($n = 134$) from Costa Rica and Panama with complete measurements (see Table 1). Lower-case letters correspond to holotypes of *creper* (c), *reventazoni* (r), and *vegetus* (v); numbered dots depict two paratypes (1–2) of Goodwin's (1945) *reventazoni*, here reassigned to *O. fulvescens*, and topotypes (3–4) of Allen's (1893) *costaricensis*. Ellipses circumscribe 95% confidence limits for specimen scores of each species; regression lines of PC II on PC I differ significantly between species in their Y-intercepts ($P < 0.001$) but not their slopes ($P = 0.556$).

tions are indicated. These include the holotypes of *Oryzomys fulvescens creper* and *O. f. reventazoni*, which cluster among samples of *vegetus* from Costa Rica and Panama, and two topotypes each of *costaricensis* and *reventazoni*, which fall among or nearer to examples of *fulvescens*. Mahalanobis distances derived from two-group discriminant function analysis associate the two holotypes as *vegetus* and classify all four topotypes as *fulvescens* (even outlier number two of *reventazoni*) according to their posterior probabilities of group membership.

Even though juveniles were omitted from our multivariate analyses, postweaning growth undoubtedly accounts for much of the scatter observed within each species

sample and for the oblique orientation of specimen scores on the first and second principal components. A similar pattern of multivariate dispersion has been recovered for other closely related, congeneric species of Muroidea (Voss & Marcus 1992), and its ontogenetic causality explicated using laboratory-raised animals in which parentage, age, sex, and equality of sample sizes have been rigorously controlled (Voss et al. 1990). Such influences on variability within and between samples, particularly balanced age and sex representation, are seldom achieved with the museum series normally accessible to an investigator. Proportion of the sexes among our samples is notably biased toward males (64% of all *f. costaricensis*; 68% of all

Table 1.—Results of principal component analysis and one-way ANOVAs performed on all intact specimens of *Oligoryzomys fulvescens* ($n = 115$) and *Oligoryzomys vegetus* ($n = 134$) from Panama and Costa Rica (see Fig. 3).

Variable	Correlations		f (species)
	PC I	PC II	
TOTL	0.94	-0.08	145.2***
TL	0.92	-0.23	225.8***
HFL	0.81	-0.32	247.8***
ONL	0.92	0.17	121.8***
ZB	0.86	0.04	151.5***
BBC	0.76	-0.33	439.5***
BOC	0.73	-0.12	131.2***
IOB	0.09	0.29	6.4**
LR	0.81	0.23	68.8***
PPL	0.82	0.27	54.5***
BPL	0.39	0.38	0.0
LD	0.83	0.13	76.3***
LIF	0.25	0.69	19.1***
BIF	0.23	0.56	11.9***
BBP	0.78	-0.06	125.4***
BZP	0.14	0.88	60.0***
LM1-3	-0.07	0.45	57.9***
WM1	0.33	0.13	3.7
LAB	0.66	-0.11	123.7***
Eigenvalue	0.041	0.013	
% Variance	52.0	16.1	

** = $P \leq 0.01$; *** = $P \leq 0.001$.

vegetus), and the number of specimens in young-, full-, or old-adult age classes does vary from OTU to OTU.

In the largest, most geographically and temporally homogeneous sample available to us (91 *vegetus* collected by R. K. Enders in Chiriquí, Panama), consistent age-related size differences are apparent, but classification by sex and sex-age interaction reveals negligible influence on mean differences (Table 2). Total length and tail length, as expected, increase among the three adult age-classes and yield highly significant mean differences, but hindfoot length does not. Among the 16 craniodental variables, the magnitude and significance levels of f -values for age-class effects are typically highest for those dimensions measured on the facial region (ZB, LR, LD, LIF), intermediate for measurements across the neurocranium

Table 2.—Results of two-way ANOVAs for 3 external and 16 cranial measurements of 91 specimens (63 ♂, 28 ♀) of *Oligoryzomys vegetus* from the valley of the Río Chiriquí Viejo, Chiriquí, Panama.

Variable	f (Sex)	f (Age)	f (inter-action)
TOTL	1.8	12.9***	0.5
TL	0.5	8.8***	0.8
HFL	0.6	2.6	0.6
ONL	1.4	29.7***	0.2
ZB	1.3	23.8***	1.1
BBC	6.9**	4.1*	0.3
BOC	0.3	8.3**	0.5
IOB	0.7	2.4	0.7
LR	0.5	21.9***	0.0
PPL	0.0	31.2***	0.2
BPL	0.2	5.7**	1.0
LD	2.1	37.1***	0.7
LIF	3.3	12.9***	0.0
BIF	0.2	8.6***	1.0
BBP	1.4	19.5***	0.2
BZP	1.2	10.1***	0.1
LM1-3	0.2	0.7	0.2
WM1	0.8	2.3	0.2
LAB	5.2*	1.5	1.1

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

(BBC, BOC, IOB), and lowest on the molars (LM1-3, WM1). These results generally parallel the patterns of covariation and growth allometry of the muroid skull documented for other species of Sigmodontinae (Voss & Marcus 1992). Although relative age may sometimes confuse the identification of individual specimens, the contribution of age-related effects is minor compared to the magnitude of interspecific differentiation between *O. vegetus* and *O. fulvescens*, for example as observed in principal component analysis (Table 3).

Table 3.—One-way ANOVAs generated for various group effects on results of principal component analysis (see Fig. 3).

Variable	f (sex)	f (age)	f (species)
PC I scores	0.6	28.3***	188.5***
PC II scores	0.5	26.3***	140.7***

*** = $P \leq 0.001$.



Fig. 4. Dorsal, ventral, and lateral views of adult crania and mandibles of: left, *Oligoryzomys fulvescens costaricensis* (USNM 541183; Panama, Chiriquí, 24 km NNE San Felix; ONL = 21.9 mm); and right, *Oligoryzomys vegetus* (USNM 541186; Panama, Bocas del Toro, 3.5 km E Escopeta; ONL = 23.5 mm).

The overall larger body size and more robust skull of *vegetus* relative to *fulvescens costaricensis* are corroborated by results of the principal component ordination. The three external and most cranial measurements exhibit high and positive correlations with the first principal component, which suggests a general size factor (Table 1), and higher scores were generated on average for specimens of *vegetus* ($\bar{X} = 0.12$) along this axis than for those of *f. costaricensis* ($\bar{X} = -0.14$). Dimensions that contribute to the separation along PC II emphasize the smaller body size (TL, HFL) and narrower skull (BBC, BOC) of *f. costaricensis*, but also reveal its relatively wide interorbit and zygomatic plate (IOB, BZP), longer and wider

incisive foramina (LIF, BIF), and more robust molars (LM1–3) as compared to examples of *vegetus* (Fig. 4). The comparatively strong loadings of LIF and BIF on PC II were unexpected, but closer examination of crania confirmed that the incisive foramina typically span about three-quarters of the diastema in *f. costaricensis* in contrast to about two-thirds in *vegetus*.

In view of the small absolute size of the skull and toothrows in *Oligoryzomys*, the magnitude of mean differences between the two species is not conspicuous (Appendix), even for dimensions where population variances are low and *f*-ratios for species effects are high (Table 1). Thus, simple univariate range limits, such as employed in keys, may

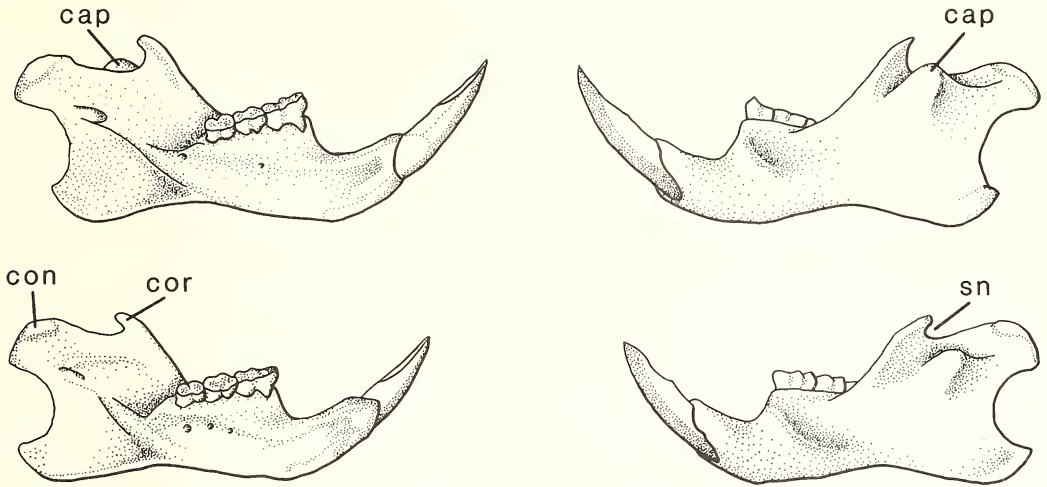


Fig. 5. Lateral and medial views of the mandibles illustrating typical development of the capsular process of: top, *O. vegetus* (USNM 541186); and bottom, *Oligoryzomys fulvescens costaricensis* (USNM 541183). Abbreviations: cap, capsular process of the lower incisor; con, condyloid process; cor, coronoid process; sn, sigmoid notch.

be uninformative for practical segregation of the species. Of the variables quantified, the larger size of *vegetus* is best appreciated in cranial length (ONL) and especially in certain width measurements (ZB, BBC, BBP). Differences in overall form and proportion, such as those reflected along PC II, are easier to grasp visually. Hence, adult specimens of *vegetus* typically exhibit a narrower interorbital constriction accentuated by laterally flaring zygoma, a slimmer zygomatic plate and hence a shallower zygomatic notch, a broader braincase and longer rostrum, more delicate molars for the size of skull, and shorter-narrower incisive foramina as compared to those of *fulvescens* (Fig. 4).

Development of the capsular process, among the few qualitative osteological traits which may serve to separate closely related muroid species, provides some discrimination of *vegetus* and *fulvescens costaricensis*. This process, which represents the posterior alveolar terminus of the lower incisor, arises from the lateral surface of the dentary. In specimens of *vegetus*, the capsular process forms a distinct knob that, with the

ascending ramus oriented in a horizontal plane, is typically observed to extend above the ventral rim of the sigmoid notch, whether viewed from a lateral or medial aspect (Fig. 5). In examples of *fulvescens*, this process is weakly pronounced, forming a lateral mound or bulge that usually ends below the ventral rim of the sigmoid notch.

This distinction is not absolute, for some specimens (16%) of *vegetus* lack the strong dorsal projection of the capsular process and a minority (7%) of *fulvescens* possess one. In approximately 20% of both species, the process terminates about level with the sigmoid notch (Fig. 6). Expression of the capsular process may correlate with age of the animal. For all individuals of *vegetus* scored ($n = 167$), there exists a strong positive association between age-class (juvenile through old-adult) and dorsal projection (below, even, above) of the capsular process (Kruskal-Wallis statistic = 38.0; $P < 0.001$). That is, individuals with the capsular process below or even with the sigmoid notch are predominantly restricted to the juvenile and young-adult age groups, whereas a capsular process extending above the notch oc-

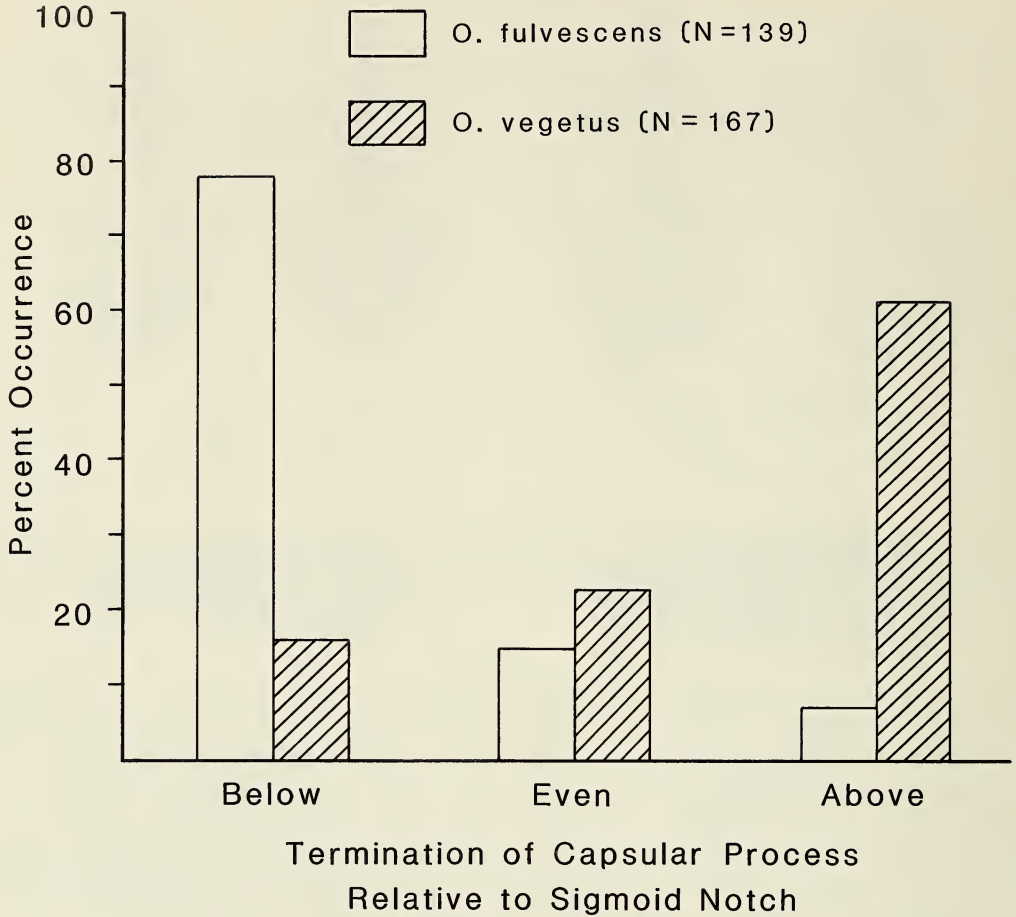


Fig. 6. Distribution of character state development of the capsular process in samples of *Oligoryzomys fulvescens costaricensis* and *O. vegetus* from Costa Rica and Panama (see Fig. 5 and text).

curs almost exclusively in full- and old-adults. Enigmatically, the parallel relationship is not supported by the same nonparametric ANOVA for all *fulvescens costaricensis* ($n = 139$; Kruskal-Wallis statistic = 4.98; $P = 0.18$). As with the utility of other distinguishing features employed at the species level, conformation of the capsular process must be considered in concert with other traits to render confident identification.

Bangs (1902) also cited the color of the incisor enamel as a diagnostic trait of *O. vegetus*. The difference—that is, pale yellowish orange in *f. costaricensis* and medium orange in *vegetus*—does seem valid as an average impression, but the contrast is

subtle and best appreciated when comparing series.

Pelage texture and color.—The two species differ in fur texture and coloration, essentially evident as a harsh and pale coat contrasted to a softer and darker one. These qualitative distinctions, although fine, are easily appreciated in freshly collected material but are less readily grasped with extremely old and faded, dust-covered museum skins.

The dorsum of *O. fulvescens* is pale tawny to reddish brown, flecked with bright buffy and dark hairs that convey a more streaked or variegated appearance (somewhat like *Reithrodontomys fulvescens*). The streaked

visual impression results from admixture of the densely black guard hairs and tricolored overhairs, which have a pronounced middle buffy band accentuated by a narrow basal plumbeous band and a very short fuscous tip. Overall, the dorsum presents a bright but pale tone and the fur is somewhat harsher to the touch.

Examples of *O. vegetus* possess more somber upperparts, evenly colored dark brown and lacking conspicuous streaking. In each overhair, the basal plumbeous band is discernably long relative to the middle buffy band, which is subdued, and the terminal tip is dusky. The resultant tone is appreciably darker than observed in typical *O. fulvescens*, and the fur is soft and fine rather than harsh. The nose, forehead, and cheeks are also darker in *O. vegetus*, and the eye ring dusky and better defined than is common in *O. fulvescens*.

A light versus dark venter distinguishes the two species. The underparts of *O. fulvescens* are pale, a whitish gray; the overhairs may be entirely white to their base, especially on the throat and chest, or with a light gray basal band. The ventral fur of *O. vegetus*, on the other hand, is dark gray in appearance, the hairs possessing a well-defined basal plumbeous band and a clear or whitish tip. A buffy overwash may occur in some specimens of either species but is more commonly encountered among samples of *O. fulvescens*. In like manner, both species have lateral ochraceous stripes but those on the sides and flanks of *O. fulvescens* are generally more prominent.

Coloration of the feet does not offer any distinguishing trait. The tops of the tarsus and metatarsus are covered with hairs that range from white to translucent and basically present a whitish appearance in both *Oligoryzomys*.

In summary, qualitative features of the skin and skull, augmented by the spatial structure inherent in multivariate summaries of the 19 mensural characters, convincingly sustain Bangs's (1902) original

perception of the existence of two morphologically similar but nonetheless distinct and separable species in western Panama. Inclusion of samples of *Oligoryzomys* from Costa Rica demonstrates the occurrence of the same two morphologies and the broader distribution of the species that we recognize as *O. vegetus*.

Relationships of *costaricensis* and *vegetus* to Other Central American *Oligoryzomys*

At the time Bangs (1902) reported his new species *Oryzomys vegetus*, previously named forms of Central American pygmy rice rats were also recognized as full species, namely *fulvescens* Saussure (1860) and *costaricensis* (Allen, 1893). In his revision of North American *Oryzomys*, Goldman (1918) established the precedent for treating all Middle American populations of *Oligoryzomys*, which he ranked as subgenus, as members of the single polytypic species *fulvescens*, and subsequent twentieth-century descriptive activity has transpired within his taxonomic framework (see subspecies and ranges, Fig. 1). In particular, systematists have routinely classified Panamanian populations of the shorter-tailed, pale-bellied form as *fulvescens costaricensis* (Goldman 1918, 1920; Hall 1981; Handley 1966).

Set against this systematic background, we naturally interpreted the morphological differentiation and sympatry of *costaricensis* and *vegetus* as indicative of the latter's specific status and continued to view the former as a subspecies of *fulvescens* (Carleton & Musser 1989, Musser & Carleton 1993). However, our casual presumption was somewhat disquieted by Joel A. Allen's (1904a:69) provocative comment in a paper that we had initially overlooked.

"Mr. Bangs informs me [given as in litt.] that he inadvertently placed the name *vegetus* on the dark form (= *costaricensis vera*) instead of on the light form, after

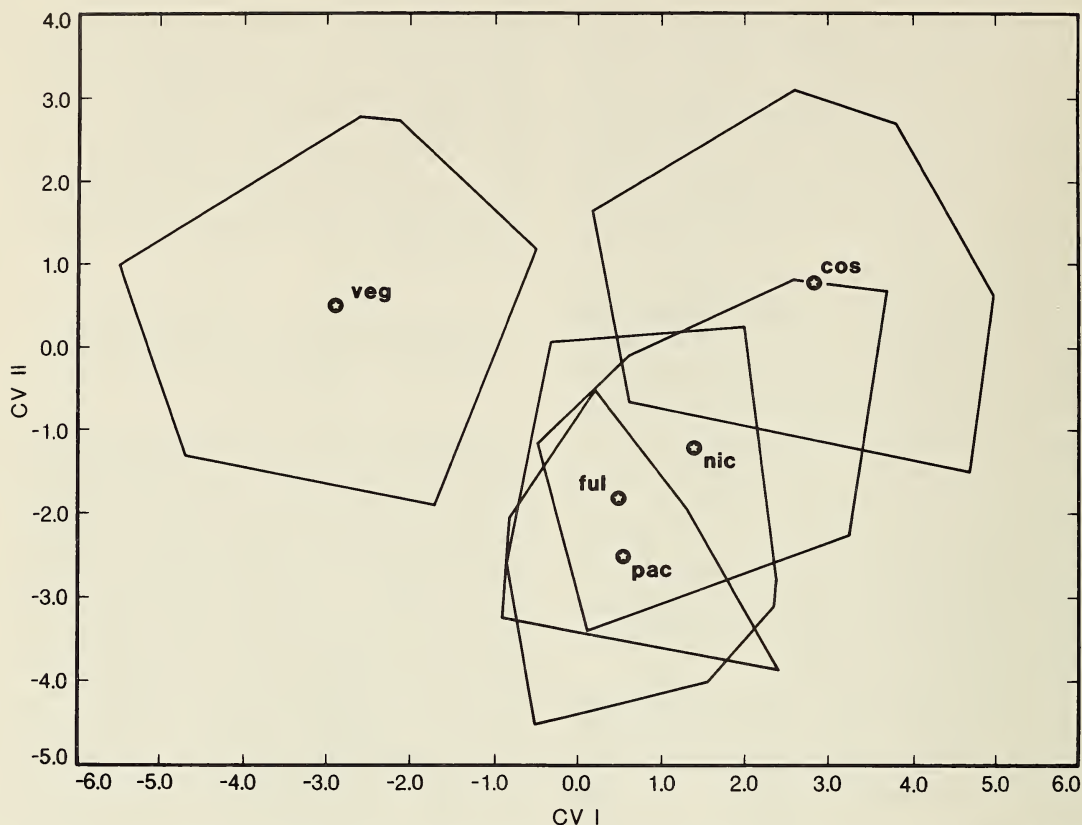


Fig. 7. Plots of first two canonical variates extracted from discrimination function analysis performed on five Central American taxa of *Oligoryzomys* and using all specimens with complete external and craniodental measurements ($n = 332$). Polygons enclose maximal dispersion of individual specimen scores around group centroids for each of five taxa (see Table 4): cos, *O. fulvescens costaricensis* ($n = 115$); ful, *O. f. fulvescens* ($n = 47$); nic, *O. f. nicaraguae* ($n = 21$); pac, *O. f. pacificus* ($n = 15$); veg, *O. vegetus* ($n = 134$).

having returned the specimens of *O. costaricensis* borrowed from this Museum [that is, AMNH], so that *vegetus* = *costaricensis* and the light form was left unnamed [emphasis ours].”

In other words, Bangs confessed to having inadvertently applied an extraneous name, *vegetus*, to the Boquete rodent that he considered identical to Allen’s (1893) *costaricensis*, while the Boquete form that he had meant to describe as new has been, by default, allocated to and subsequently known as *fulvescens costaricensis* (for example, Goldman 1920, Hall 1981, Handley 1966). Curiously, Goldman supplied no indication

that he was aware of the supposed mix-up with regard to the naming of *vegetus*, either in his revision of *Oryzomys* (1918) or in his publication on the mammals of Panama (1920).

Allen’s (1904a) allusion to an unfortunate lapsus by Mr. Bangs reopens the issue of which taxon, *costaricensis* or *vegetus*, if either, intergrades with northern populations of *Oligoryzomys fulvescens*, to which problem we now turn. In assessing these relationships, we included specimens from Veracruz, Mexico, as a comparative standard for Saussure’s (1860) *fulvescens* s. s. Representatives of other northern subspecies were selectively sampled: *nicaraguae* Allen

(1910) because of its contiguous geographic position to *costaricensis*; and *pacificus* Hooper (1952) because of Jones & Engstrom's (1986) suggestion that it may link with more southerly-distributed, Pacific-coast populations of *fulvescens*.

Goldman (1918) formally recognized, aside from the nominate race, four subspecies of *Oryzomys (Oligoryzomys) fulvescens*: *costaricensis* Allen (1893) (with *nicaraguae* Allen, 1910, in full synonymy), *lenis* Goldman (1915), *mayensis* Goldman (1918), and *vegetus* Bangs (1902). His remarks under the various subspecific accounts clearly affirm that he viewed *costaricensis* as most similar to the nominate form *fulvescens*.

Our morphometric evaluations reinforce Goldman's (1918) general estimation of phenetic resemblance and support a hypothesis of consanguinity among Central American races currently arranged under *Oligoryzomys fulvescens* (that is, excepting *O. vegetus*). Although much variation exists within and among geographic representatives of *O. fulvescens*, these subspecific taxa considerably overlap one another in multivariate space, and all four are wholly set apart from specimens of *O. vegetus* (Fig. 7). In group assignments according to posterior probabilities of membership, specimens of the four subspecies were variously distributed among one another, but none was misclassified with *vegetus*, or vice versa. Clustering of OTU means also emphasizes the integrity of samples of *O. vegetus* as distinct from those representing the four geographic races of *O. fulvescens* (Fig. 8).

The three external measurements and most cranial variables contribute more or less equally to the hiatus along the first canonical variate and, by the sign and magnitude of their loadings (Table 4), underscore the fundamentally larger size of *vegetus* as contrasted to specimens of *fulvescens*, including *costaricensis*. Certain cranial dimensions (BZP, IOB, LM1-3), as divulged in the PCA, depart from this pattern and appear relatively, in some OTUs ab-

Table 4.—Results of discriminant function analysis performed on all intact specimens of *Oligoryzomys f. fulvescens* ($n = 47$), *O. f. costaricensis* ($n = 115$), *O. f. nicaraguae* ($n = 21$), *O. f. pacificus* ($n = 15$), and *Oligoryzomys vegetus* ($n = 134$) (see Fig. 7).

Variable	CV I	CV II	$f(\text{taxon})$
TOTL	-0.63	0.41	62.0***
TL	-0.69	0.44	89.1***
HFL	-0.73	0.18	77.5***
ONL	-0.58	0.39	55.8***
ZB	-0.62	0.32	54.7***
BBC	-0.81	0.36	139.4***
BOC	-0.55	0.49	56.1***
IOB	0.03	0.75	35.3***
LR	-0.48	0.33	31.3***
PPL	-0.37	0.28	20.5***
BPL	-0.09	0.53	17.8***
LD	-0.48	0.29	27.6***
LIF	0.17	0.24	5.5***
BIF	0.16	-0.03	2.7*
BBP	-0.59	0.46	61.3***
BZP	0.38	0.20	17.3***
LM1-3	0.29	0.64	34.8***
WM1	-0.19	0.51	21.3***
LAB	-0.56	-0.07	35.9***
Canonical correlations	0.93	0.73	

* = $P \leq 0.05$; *** = $P \leq 0.001$.

solutely, greater in certain examples of *fulvescens*. For instance, Goldman (1918), in comparing *costaricensis* to *fulvescens* proper, cited the wider and longer molar rows of the former as its most distinctive character and one that approached *vegetus* in size. Although the correctness of Goldman's assessment does hold in simple univariate comparisons, a multivariate perspective demonstrates the proportionally large molar rows possessed by individuals of *costaricensis*, a shape feature which clearly aligns it with other representatives of *O. fulvescens*, not *O. vegetus*.

Qualitative agreements too—like cranial shape and proportions and pelage color and texture—support the affiliation of *costaricensis* with *fulvescens* and other northern races. Termination of the incisor capsule below the sigmoid notch is the common

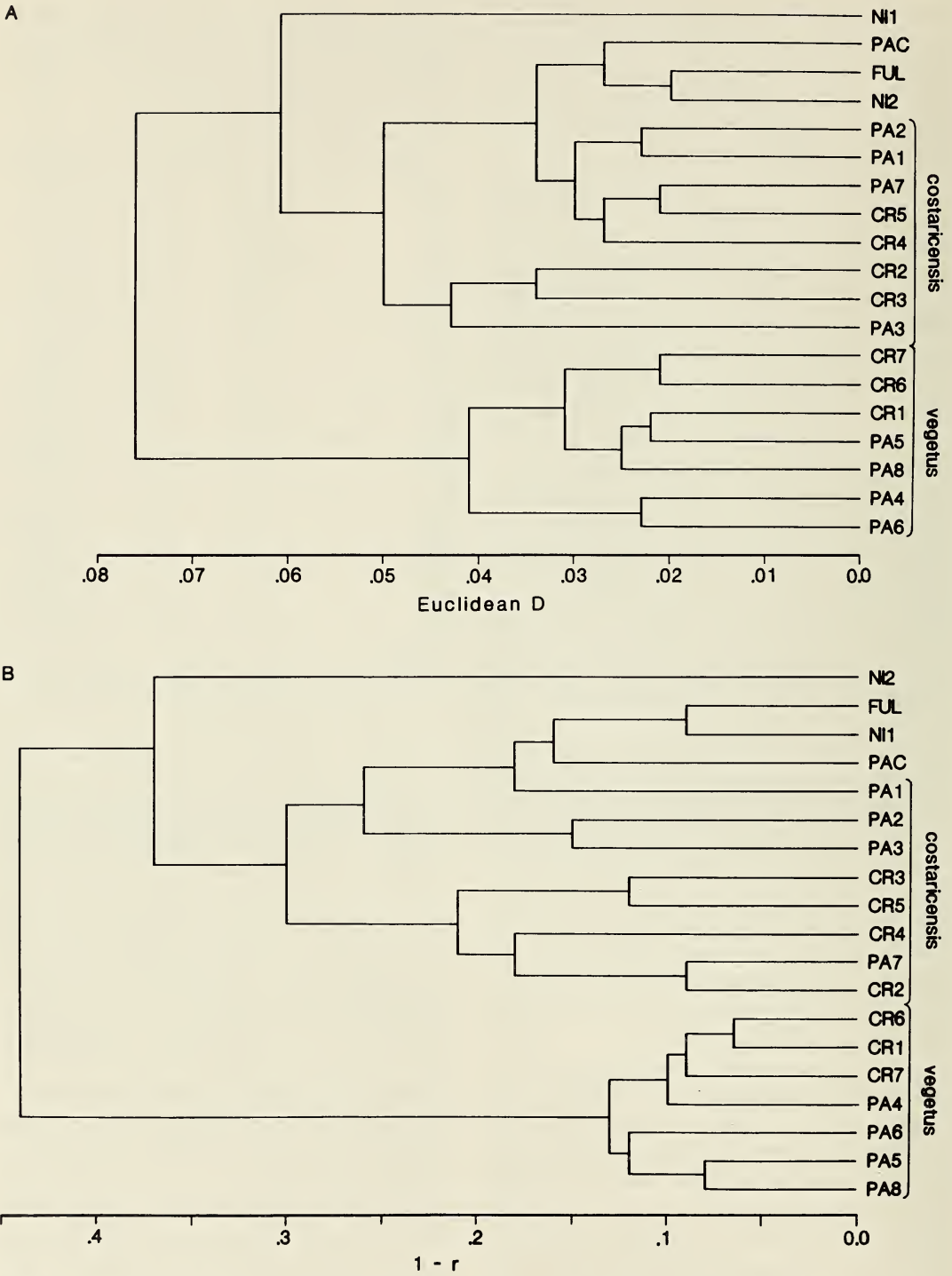


Fig. 8. UPGMA clustering of log-transformed samples means for the 19 OTUs of Central American *Oligoryzomys* identified in the Materials and Methods, using both a Euclidean distance coefficient (A) and the Pearson correlation coefficient (B).

condition in *f. fulvescens* (56% of 36 specimens scored) and *f. nicaraguae* (67% of 33 specimens), but these percentages are lower than that derived for our larger sample of *f. costaricensis* (78% of 139 specimens). Thus, the development of the capsular process in the former populations, while in the direction of agreement with *f. costaricensis*, is less decisive as a basis for discrimination from *O. vegetus*.

In summary, both morphometric comparisons and discrete character traits indicate the close kinship and probable conspecificity of *costaricensis* with northern *O. fulvescens*. Although we advise the continued affiliation of *costaricensis* as a subspecies of *O. fulvescens*, we stress the need for stronger empirical analyses of relationship and status among populations of *fulvescens* (see discussion below). Aside from such uncertainties involving *O. fulvescens*, and whether intended or not, Bangs (1902) did not err in selecting an individual of the "dark form" as the type of his new species *Oligoryzomys vegetus*.

Distribution and Zoogeography

In reinstating *vegetus* as a valid species of *Oligoryzomys*, Carleton & Musser (1989) at the time viewed its distribution as restricted to the highlands of western Panama, principally in the region of Volcán de Chiriquí. Although zoogeographically plausible, they, and later Musser & Carleton (1993), overlooked its presence in the contiguous mountain systems of Costa Rica. Such a distributional picture is confirmed by the renewed study of museum specimens, including evidence provided below for the junior synonymy of certain *Oligoryzomys*—namely *creper* Goodwin (1945) and *reventazoni* Goodwin (1945)—described from the middle and upper highlands of Costa Rica.

The species *Oligoryzomys vegetus*, or sprightly pygmy rice rat as christened by Bangs (1902), inhabits the rugged, mountainous spine of central Costa Rica and

western Panama (Fig. 9). Specimens at hand document its geographic range from the northernmost extent of the Cordillera de Tilarán (Monteverde and environs), through the cordilleras Central and Talamanca, to the Cordillera de Chiriquí (at least to the vicinity of Cerro Bollo). We have searched for examples of *O. vegetus* among other museum series of *O. fulvescens* (in addition to those listed herein) from the highlands of Nicaragua, Guatemala, and southern Mexico but have found only *fulvescens* proper in these regions. We therefore believe that our locality records circumscribe the principal geographic distribution of *O. vegetus* (Fig. 9), although it may be expected farther east in westcentral Panama and may be sought on the highest peaks of the Cordillera de Guanacaste in northern Costa Rica (but see below).

The known altitudinal occurrence of *Oligoryzomys vegetus* extends from 840 m (valley of the Río Peñas Blanca, Costa Rica) to over 3000 m (below the summits of Volcán Irazú and Cerro de la Muerte, Costa Rica). Most collecting localities lie between 1000 and 2000 m. *Oligoryzomys vegetus* does not penetrate the tropical lowlands of Costa Rica and Panama where *O. fulvescens* commonly occurs (Fig. 9). Within these countries, the latter species is found from near sea level to approximately 2000 m. Although most localities of *O. f. costaricensis* occur from 750 m to 1500 m, as portrayed in Fig. 10, the low incidence of records below 750 m is biased by the infrequency of elevational notation by collectors (for example, the numerous lowland localities in eastern Panama and northern Costa Rica); whereas, collecting stations in the middle and upper highlands more commonly bear, for whatever reason, altitudinal information. Thus, histograms of altitudinal occurrence (Fig. 10) are dominated by the long history of mammalogical field work in the mountains of central Costa Rica and western Panama.

These regions, not unexpectedly, also contain most locations of documented sym-

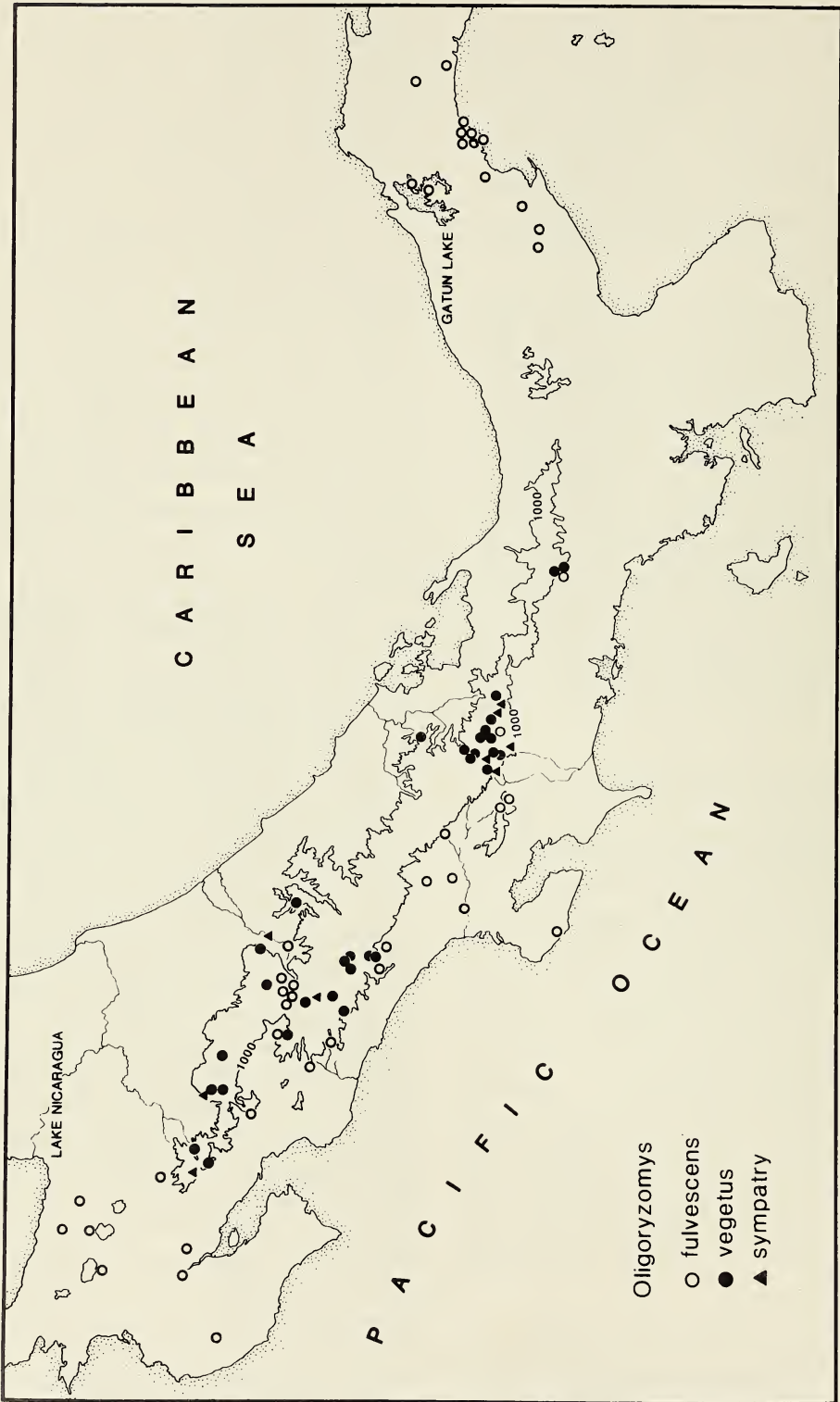


Fig. 9. Geographic distribution of *Oligoryzomys fulvescens* and *O. vegetus* in Costa Rica and Panama based on specimens examined herein. Solid line corresponds to the 1000-meter contour.

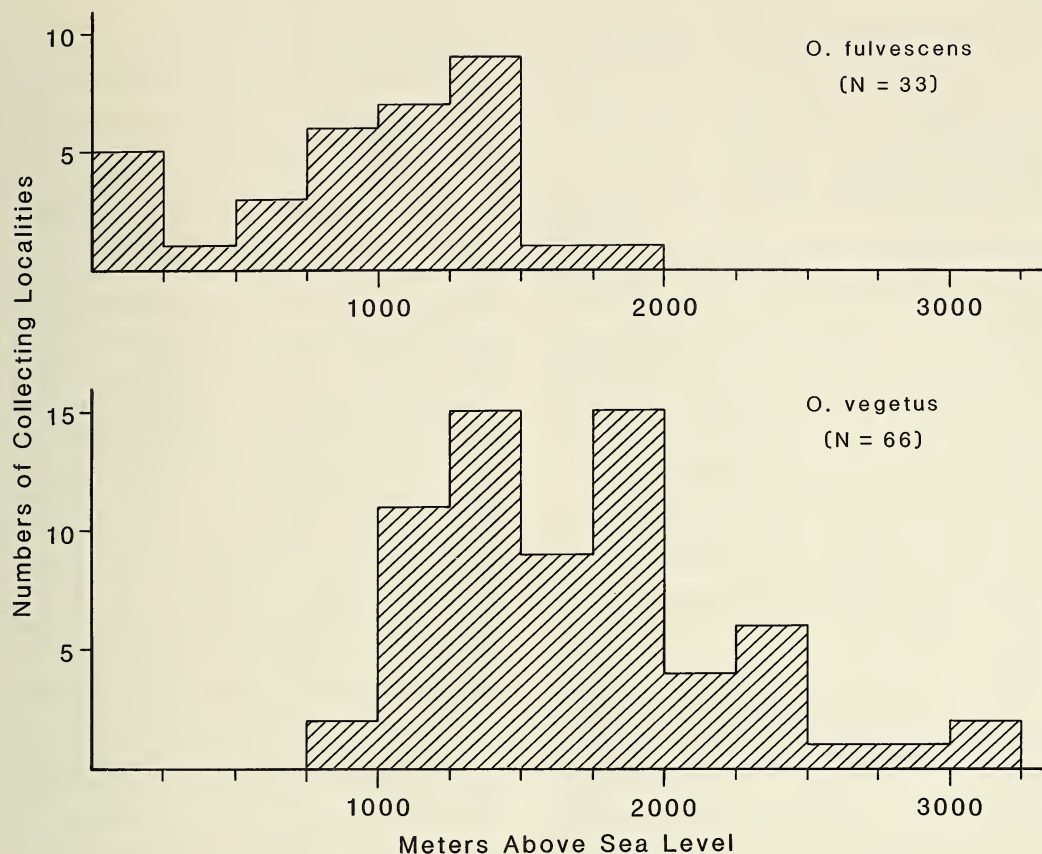


Fig. 10. Frequency distributions illustrating occurrence of collecting localities with recorded elevations for samples of *Oligoryzomys fulvescens* and *O. vegetus* from Costa Rica and Panama.

patry of *O. vegetus* and *O. f. costaricensis*, especially along the upper drainage basins of the Río Reventazón, Costa Rica, and the Río Chiriquí Viejo, Panama. In addition to Bangs's (1902) original discernment of sympatry at Boquete, Panama, we have encountered examples of *O. vegetus* and *O. f. costaricensis* intermixed at several other sites, both in Costa Rica (El Muñeco, Monteverde, Lajas) and in Panama (Río Chebo, Río Gariche, Finca Lerida, Finca Santa Clara, Río Santa Clara). Indeed, as argued below, Goodwin's (1945) type series of *Oryzomys fulvescens reventazoni*, from Santa Teresa Peralta, Costa Rica, is itself a composite, the holotype synonymous with *O. vegetus* and the four paratypes referable to

O. fulvescens. Almost all sites of sympatry or contiguous allopatry lie within the elevational zone from 1000 to 1500 m.

In his insightful biogeographic study of Costa Rican rodents, McPherson (1985:224) characterized *fulvescens* as virtually ubiquitous within the country, occurring throughout most biotic zones, and having "geographical and elevational distributions . . . greater than those of any other species in Costa Rica." His geographical and ecological summation, like the earlier erroneous definition of "*Oryzomys fulvescens*," was a misleading composite based on data from two biological species. In fact, reassortment of McPherson's, and our own, Costa Rican localities by correct specific identifications

reveals far narrower altitudinal and ecological occurrences of the two *Oligoryzomys* that correspond intelligibly with well-defined climatic, vegetational, and physiographic associations. Populations of *O. fulvescens costaricensis* predominantly occur within Tropical and Premontane life zones (sensu Holdridge 1967); whereas, those of *O. vegetus* are principally confined to Lower Montane and Montane formations. Most instances of sympatry involve sites classified as Premontane Wet Forest and Premontane Rain Forest, although overlap at lower (Tropical Wet Forest-Upper Transition) and higher (Lower Montane Wet Forest) life zones does occur. The deeper, softer pelage of *O. vegetus* is consistent with its higher-elevation affinity and presumably confers greater insulative properties for a small rodent living in wet, cool environments.

Within these broadly characterized forest domains, pygmy rice rats prefer grassy or shrubby microhabitats placed within forest clearings or at woodland edges, often along small streams or near other aquatic settings. Specific habitat notations on skin tags commonly reference "dense grass at edge of clearing near stream," "second-growth scrub at edge of clearing," "dense grass beside small stream in forest," and "under tall weeds and raspberry bushes." In view of their proclivity for early successional stages, both species of *Oligoryzomys* seem to adapt readily to a variety of second-growth habitats and to prosper around active or abandoned agricultural fields and pasturelands. We cannot glean suitably detailed information from field catalogs and skin labels that would suggest microhabitat segregation of the two *Oligoryzomys* at localities of sympatry, perhaps because field workers were seldom aware that two species might be encountered in their traplines. At one such place, El Muñeco in Costa Rica (1100–1200 m), Austin Smith trapped five specimens of *Oligoryzomys*, all initially identified as *O. fulvescens costaricensis*. Two of these prove

to be *O. fulvescens*, both caught in "Caribbean rain forest in brush," and three are *O. vegetus*, one each trapped in "Caribbean rain forest in sugar cane," "pasture in cloud forest zone," and "Caribbean cloud forest." *Oligoryzomys*, species indeterminate, has been described both as terrestrial (e.g., Handley 1966) and as semi-arboreal (e.g., Timm et al. 1989), and has been observed to climb nimbly upon small limbs and branches in dense undergrowth (McPherson 1985). The larger hindfeet and relatively longer tail of *O. vegetus* predict more highly developed scansorial abilities in this species. Beyond these natural history anecdotes and generalities, detailed field studies must be conducted to shed light on specific ecological requirements and habits of the two *Oligoryzomys* in areas of syntopy.

Although the morphological similarity between *Oligoryzomys vegetus* and Central American *O. fulvescens* has engendered years of taxonomic confusion, the two may not prove to be sister species. In fact, the closest specific relative of *O. vegetus* may inhabit the northern Andes of South America. In his description, Bangs (1902:36) speculated that *vegetus* "may prove to be only a northern subspecies of *O. dryas humilior* Thomas of Colombia, Bogota region to Santa Marta region." The forms *dryas* and *humilior*, however, are junior synonyms of *Microryzomys minutus*, a species of a very distinctive oryzomyine genus related to *Oligoryzomys* (see Carleton & Musser 1989). A more plausible candidate is suggested by Osgood (1912), who named a new pygmy *Oryzomys*, *O. griseolus*, from the Páramo de Tama in westernmost Venezuela. Osgood, who had available samples of geographically contiguous *Oligoryzomys* like *navus* and *tenuipes*, thrice mentioned *O. vegetus* of western Panama as bearing the greatest resemblance to his new species. The question of their phylogenetic stature to one another, like the need for improved delimitation of species and phylogenetic systematics of South American *Oligoryzomys* in

general, still warrants much basic investigation (see Carleton & Musser 1989). However, biogeographic consideration of other mammals, as well as other vertebrates, restricted to these Costa Rica-Panamanian mountains suggests that such a northern Andean connection is reasonable.

The distribution of *Oligoryzomys vegetus*, as now understood, accords closely with a region of Middle American topography already recognized by zoogeographers and variously labeled the Costa Rica-Chiriquí Highlands (Slud 1964), the Talamancan Province (Savage 1966), or the Cordilleran Faunal Area (McPherson 1985, 1986). (Middle America is here understood to include Central America north of the Panamanian isthmus and most of Mexico exclusive of the Mesa Central.) The middle- to high-elevation mountains in Costa Rica and western Panama, harboring cool and perennially moist forests, have figured prominently in the historical zoogeography and phyletic diversification of Central American amphibians and reptiles (Savage 1966, 1982) and birds (Slud 1964, Stiles 1983), vertebrate groups which contain a large number of species and genera endemic to the region. Small terrestrial mammals do not exhibit such high degrees of endemism as these other vertebrates; nonetheless, the area has played an important role in their phylogenetic history as well, especially as demonstrated for Rodentia by McPherson (1985, 1986). Many rodent species either reach their southern or northern limits of distribution in the Cordilleran Faunal Area or are hypothesized to have originated there in situ.

Review and enhancement of McPherson's (1985) taxonomic and distributional data indicate that at least one genus (*Syntheosciurus*), 14 species, and two strongly differentiated subspecies of small mammal are limited to the mountains of Costa Rica and western Panama and their humid forest associations (Table 5). Most of these taxa occur in both the Chiriquí region of western Panama and the Talamancan

Table 5.—Insectivora, Lagomorpha, and Rodentia endemic to highlands of Costa Rica and western Panama.

Taxon	Cordilleras			
	Tilarán	Central	Talamanca	Chiriquí
Soricidae				
<i>Cryptotis endersi</i> ^a			?	X
<i>C. gracilis</i> ^b	X	X	X	X
<i>C. nigrescens</i> ^c	X	X	X	X
Leporidae				
<i>Sylvilagus dicei</i> ^d			X	X
Sciuridae				
<i>Syntheosciurus brochus</i> ^e		X	X	X
Geomyidae				
<i>Orthogeomys cavator</i> ^f			X	X
<i>O. heterodus</i> ^g		X	X	
Heteromyidae				
<i>Heteromys oresterus</i> ^h			X	
Muridae				
<i>Rheomys raptor hartmanni</i> ⁱ	X	?	X	X
<i>R. underwoodi</i> ^j		X	?	X
<i>Oryzomys devius</i> ^k		X	X	X
<i>Oligoryzomys vegetus</i> ^k	X	X	X	X
<i>Sigmodontomys aphrastus</i> ^l			X	X
<i>Reithrodontomys b. brevirostris</i> ^m		X	X	
<i>R. creper</i> ⁿ	X	X	X	X
<i>R. rodriguezii</i> ^o		X	X	
<i>Scotinomys xerampelinus</i> ^p		X	X	X

Sources.—a: Choate (1970); b: Woodman & Timm (1992), N. Woodman (pers. comm.); c: Woodman & Timm (1993); d: Diersing (1981); e: Enders (1980); f: Hafner (1991); g: Rogers & Rogers (1992); h: Reid & Langtimm (1993), Voss (1988); i: Voss (1988); j: Gardner (1983); k: This study; l: Musser & Carleton (1993); m: Hooper (1952), McPherson (1985); n: Hooper (1952), Timm et al. (1989); o: McPherson (1985), Timm et al. (1989); p: Hooper (1972).

cas of southcentral Costa Rica. Fewer species are known to occur throughout the four highland areas, but there is reason to doubt that they necessarily would. Geological evidence (summary in Castillo-Muñoz 1983) supports the greater antiquity (Oligocene-Miocene) of the Talamanca-Chiriquí ranges as compared to the younger Central and Tilarán cordilleras (late Pliocene-Pleistocene). Some have attributed the high endemism to the possible isolation of the Talamanca-Chiriquí region as an island, or series of islands, within the Panamanian portal prior

to complete closure and late-Pliocene formation of the landbridge (McPherson 1985, 1986; Slud 1964; Stiles 1983). Vouchered evidence for the expected occurrence of some species within certain mountain ranges is yet lacking, an omission that prescribes the continuing need for basic faunal survey. Also lacking is recent systematic investigation of other mammalian groups with highly disjunct Middle American distributions and distinctive geographic races limited to these southern highlands. Renewed revisionary focus on taxa such as *Cryptotis parva*, *Peromyscus mexicanus*, *Reithrodontomys mexicanus*, *R. sumichrasti*, and *Scotinomys teguina* will likely augment the amount of endemism thus far apparent among small mammals.

Most of the 17 species-group taxa (Table 5) represent genera that are either wholly endemic to Middle America (*Syntheosciurus*, *Orthogeomys*, *Heteromys*, *Rheomys*, and *Scotinomys*), or genera whose species diversity persuasively implicates a Middle American origin and subsequent radiation into temperate North America and northwestern South America (*Cryptotis*, *Reithrodontomys*—see Choate 1970, and Hooper 1952, respectively). Except for *Rheomys* (see Voss 1988), these Middle American endemics have tribal-, subfamily-, or family-level phyletic affinity with species that are otherwise North American in distribution and origin. However, like *Rheomys*, the three species of Oryzomyini (sensu Voss & Carleton 1993) appear to represent Central American elements of groups that are essentially South American in origin and principal differentiation. *Oryzomys devius* is the northernmost outlier of the *albigularis* species-group, a complex which is predominantly northern Andean in diversity and distribution (for example, see Patton et al. 1990) and whose morphology exhibits generic-level differentiation from other oryzomyines. Musser & Carleton (1993) provisionally associated the poorly known species *aphrastus* with the genus *Sigmodonto-*

mys, whose type species *alfari* is distributed over lowland forest in southern Central America and northwestern South America, where it reaches western and northern Andean slopes but not eastern ones. The form *aphrastus* actually may bear closer kinship to another enigmatic, little known species, *Oryzomys hammondi* of northwestern Ecuador (for example, see Hershkovitz 1948). And the putative sister species of *Oligoryzomys vegetus* may be plausibly sought, as suspected by Osgood (1912), among northern Andean members of the genus. Biogeographic evaluations of other vertebrates lend support to the possibility that the vicariant sister-groups to many taxa endemic to the Costa Rica-Chiriquí highlands occur in South America (Savage 1966, 1982; Slud 1964).

The conjectural tone of the previous paragraph exposes the weaknesses of our current systematic understanding of many neotropical rodents—confusion over their morphological identity, meagre specimen-based knowledge of their distributions, and absence of explicitly defended statements of their phylogenetic relationships. Such systematic and biogeographic speculation should be tested by character data and viewed from a cladistic perspective. Improved species definition of forms like *Oligoryzomys vegetus* is an elemental step toward these goals.

Taxonomy

Oligoryzomys vegetus (Bangs)

- Oryzomys* (*Oligoryzomys*) *vegetus* Bangs, 1902:35 (type locality—Panama, Volcán de Chiriquí, Boquete, 4000 ft; holotype—MCZ 10298).—Miller, 1912:177.
- Oryzomys costaricensis*.—Allen, 1904a:69.
- Oryzomys fulvescens vegetus*.—Goldman, 1918:93.—Goldman, 1920:102.—Miller, 1924:363.—Goodwin, 1946:396.—Miller & Kellogg, 1955:441.—Hall & Kelson, 1959:568.—Handley, 1966:781.—Hall, 1981:622.

Oligoryzomys vegetus.—Carleton & Musser, 1989:71.—Musser & Carleton, 1993:718.

Oryzomys fulvescens creper Goodwin, 1945:2 (type locality—Costa Rica, Cartago, Volcán Irazú, 9400 ft; holotype—AMNH 141199).—Goodwin, 1946:396.—Miller & Kellogg, 1955:440.—Hall & Kelson, 1959:568.—Musser & Carleton, 1993:718.

Oryzomys fulvescens reventazoni Goodwin, 1945:3 (type locality—Costa Rica, Cartago, Santa Teresa Peralta; holotype—AMNH 141891).—Goodwin, 1946:397.—Miller & Kellogg, 1955:440.—Hall and Kelson, 1959:568.—Musser & Carleton, 1993:718.

Emended diagnosis.—A species of *Oligoryzomys* characterized by relatively soft and fine pelage, dorsum a somber, dark brown, without prominent streaking or grizzling, and underparts dark gray; tail dusky, monocolored for most of its length except slightly paler near the ventral base; size medium (HFL ca. 22–25 mm, ONL ca. 22–24 mm) for the genus with relatively long tail (usually >110 mm in adults), about 140% of head-and-body length; skull relatively broad across zygomatic arches (ca. 11.3–12.5 mm) and braincase (ca. 10.5–11.0 mm), zygomatic plate and interorbital constriction correspondingly narrow; molar toothrows (2.7–3.0 mm) appear delicate for size of skull; capsular process of dentary well developed.

Distribution.—Intermediate to high elevations (840 to <3000 m) in the mountains of Costa Rica (cordilleras Tilarán, Central, and Talamanca) and western Panama.

Remarks.—Goodwin (1945) named two Costa Rican subspecies of *Oryzomys fulvescens* that we herein reallocate to *Oligoryzomys vegetus*. He (1945:2) characterized *creper* as “A rather small, dark-colored, long-tailed *Oligoryzomys*, smaller than *vegetus* Bangs, with noticeably smaller feet and darker color.” Examples of *vegetus* from

Costa Rica do average smaller than our samples from western Panama but not inordinately so (Appendix), and they unambiguously cluster with Panamanian OTUs of *vegetus* as opposed to geographically proximate representatives of *fulvescens costaricensis* (Fig. 8). Craniodental proportions and qualitative features, including development of the capsular process, of the type specimen of *creper* inarguably place it within the morphological range observed for Bangs’s (1902) *vegetus* (see Fig. 3), which condition supports their synonymy. Except for our disagreement over specific assignment and status, Goodwin’s description and comparisons of *creper* are apt, and most AMNH specimens from the central highlands of Costa Rica that he (1945, 1946) referred to the subspecies we accept as *vegetus*.

Oryzomys fulvescens reventazoni, Goodwin’s other Costa Rican subspecies, presents a less clearcut interpretation, in part due to the uniformly young age of the five specimens composing the type series. Defining characters, as stated by Goodwin (1945:3), recall those of *creper*: “A very small, dark-colored pygmy rice rat. Similar in general appearance to *O. f. creper* but much smaller and tail shorter.” Goodwin (1945, 1946) repeatedly emphasized the striking resemblance, except for size, between the type specimen of *reventazoni* and that of *creper*. In fact, many distinctions he ascribed to the two holotypes can be reasonably attributed to age-related size differences, for the holotype of *creper* is a very old adult with flatly worn molars, whereas that of *reventazoni* is a much younger animal in fresh adult pelage. Goodwin simultaneously noted the still smaller size and paler coloration, with white underparts, of his four topotypes of *reventazoni*; their size and pelage impress us only as young individuals of *fulvescens*, which is known to occur with *vegetus* elsewhere in the upper valley of the Río Reventazón (see Specimens Examined). Finally, results of principal

component analysis substantiate the closer morphometric agreement of the type of *reventazoni* to examples of *vegetus* and of the two measurable topotypes to those of *fulvescens* (Fig. 3). We conclude that Goodwin's type series is a composite. The identity of the type specimen (AMNH 141891), as name bearer of the taxon, dictates the relegation of *reventazoni* to subjective junior synonymy under *O. vegetus*; the four topotypes (AMNH 140364–5, 141890, 141892) are reassigned to *O. fulvescens costaricensis*.

Specimens examined.—352, as follows.

Costa Rica: Provincia de Alajuela, Cataratos San Carlos (AMNH 141941–2); Monteverde Cloud Forest Reserve, valley of Río Peñas Blancas, La Esperanza, 840 m (KU 143399); Lajas Villa Quesada (AMNH 139736–43, 140363); Tapasco (AMNH 139804–6); Volcán Poas, 2000 m (UMMZ 123200); Zarcero, 6500 ft (FMNH 43990). Provincia de Cartago, Estrella de Cartago, 4500 ft (UMMZ 64131–2); Volcán Irazú, 9400 ft (AMNH 141199); Volcán Irazú, 0.25 mi N Hotel Robert, 2575 m (UMMZ 116903); Moravia, 1116 m (UMMZ 111983, 112283–4); El Muñeco, 10 mi S Cartago, Río Navarro, 3700, 3800, and 4000 ft (UMMZ 67310, 67312–3); El Muñeco, 13 km S Cartago (KU 27017); Salsipuedes, Pan Am Hwy, 2730 m (UMMZ 123380); El Sauce Peralta (USNM 250394–5); Santa Teresa Peralta (AMNH 141891). Provincia de Limón, Río Teribé, Valle El Silencio, Río Cotón, 8000 ft (USNM 539895–907). Provincia de Puntarenas, Monteverde, 1400–1465 m (KU 142063, 142066–8, 143315, 143398; UMMZ 115425, 116904–8, 117102–4; USNM 566458); Monteverde, Cerro Amigos, 1760 m (KU 142064–5); Monteverde, Reserva Bosque Nuboso, La Ventaña (USNM 559054); Vera Cruz, 1320 m (KU 143502). Provincia de San José, El Copey de Dota, 6000 ft (UMMZ 64039–40, 65071); Los Higuerones, Escazú (AMNH 137291, 138020–6, 138076–9); Cerro de Buena Vista, 10,342 ft (AMNH 9567/7909);

Cerro de la Muerte, summit (on Pan Am Hwy), 10,200 ft (UMMZ 112280); Cerro de la Muerte, 5.5 mi S (via Pan Am Hwy) summit, La Georgina (UMMZ 112281–2); Cerro de la Muerta, Villa Mills (UMMZ 115426); 9 mi N (via Pan Am Hwy) San Isidro del General, 4800 ft (UMMZ 111970); 11 mi N (via Pan Am Hwy) San Isidro de General, 5200 ft (UMMZ 111971–5, 112279); San Joaquín de Dota, 3800 and 4000 ft (UMMZ 62882–3, 62887–8).

Panama: Provincia Bocas de Toro, northeast of Boquete, near Río Cylindro, 2380 m (USNM 516745); 3 km NE Escopeta, Quebrada de los Gatos, 1375 m (USNM 541172); 3.5 km E Escopeta, Cerro Bollo, 1800–1856 m (USNM 541186–8); 20 mi SSW Changuinola, upper Río Changena, Rancho Mojica, 4800, 5000, and 5400–5600 ft (USNM 319316–26); Fish Camp, 4900 ft, 08°58'N/82°40'W (USNM 520730–5); Upper Camp 1975, 08°56'N/82°42'W (USNM 520736); 17.5 km NNW El Hato del Volcán, NE Cerro Pando, 2180 m (USNM 516758–9); 25 km NNE San Félix, 1425–1500 m (USNM 541184–5). Provincia de Chiriquí, Bambito, 5800 and 5900 ft (USNM 314355, 314777); Boquete, 4000, 4500, and 4800 ft (AMNH 18825–8, 18834–6; FMNH 14298, 14302, 14304–6, 18518–9; MCZ 10297–8, 10300–4, 10308–10; USNM 242339); head of Río Candela, 17 km NNW El Hato del Volcán, 2000 m (USNM 516764); Casita Alta, 7000 ft (ANSP 18546–7, 18624); Río Chebo (ANSP 18514, 18516–7, 18522); Río Chiriquí Viejo, 3800 ft (ANSP 18523–5, 18945), 1600–1850 m (UMMZ 116911–8, 117100); Cotito Hot Springs (USNM 396546); Cylindro (ANSP 20956); Río Gariche, 5350 ft (ANSP 18409, 18618–23); Hortigal (ANSP 20825, 20830, 20968, 21024); Finca Lerida (ANSP 20761, 20768, 20803, 20871, 20921, 20923); Osta Clara Camp (ANSP 18334); Cerro Pando, 4100 ft (AMNH 147790; ANSP 17853–9); Peña Blanca (ANSP 20852, 21039); Cerro Punta, 1825 m (ANSP 18744, 18746–54, 18756–7; UMMZ

116921); 0.5 mi W Cerro Punta, 1825 and 1880 m (UMMZ 116919–20); 0.5 mi SE Cerro Punta, Volcán de Chiriquí, 2000 m (UMMZ 116922–5); Cerro Punta, Boquete Trail, 7000, 7700, 7750, and 7800 ft (USNM 323883–97); Cerro Punta, Casa Tilley, 5300 ft (USNM 314344, 318429–30); Cerro Punta, Finca Martinz, 6800 ft (USNM 314345–54); Finca Santa Clara, 14.5 km NW El Hato de Volcán, 1200–1500 m (USNM 395547, 516742, 516757, 516761, 516763, 516767, 516774, 537618); Río Santa Clara, 4150 ft (ANSP 18628, 18634, 18637–8); Siola, 4100–4300 ft (ANSP 17852, 18389–91, 18532, 18543, 18550–611, 18944, 18956–8, 18960, 18964–5, 18969, 18971, 18978, 18981–3, 18989, 18991, 18994, 18998–9, 19081–2, 19088–9); locality unknown (AMNH 173903; ANSP 17825, 21046).

Oligoryzomys fulvescens (Saussure)

H. [esperomys] fulvescens Saussure, 1860: 102 (type locality—Mexico, Veracruz, vicinity of Orizaba—as subsequently restricted by Merriam, 1901:295).

Oryzomys costaricensis Allen, 1893:239 (type locality—Costa Rica, Puntarenas, El General, 2150 ft; holotype—AMNH 9581/7922).

Oryzomys delicatus Allen and Chapman, 1897:19 (type locality—Trinidad, Caparo; holotype—AMNH 7317/5925).

Oryzomys navus Bangs, 1899:9 (type locality—Colombia, Magdalena, Sierra Nevada de Santa Marta, Pueblo Viejo, 8000 ft; holotype—MCZ 8107).

Oryzomys navus messorius Thomas, 1901: 151 (type locality—British Guiana [Guyana], Kanuku Mountains; holotype—BMNH 1901.6.4.97).

Oryzomys tenuipes Allen, 1904b:328 (type locality—Venezuela, Mérida, Mérida, 1630 m; holotype—AMNH 21330).

Oryzomys (Oligoryzomys) nicaraguae Allen, 1910:100 (type locality—Nicaragua, Matagalpa, Vijagua; holotype—AMNH 29543).

Oryzomys (Oligoryzomys) munchiquensis Allen, 1912:85 (type locality—Colombia, Cauca, La Florida, 7700 ft; holotype—AMNH 32603).

Oryzomys fulvescens lenis Goldman, 1915: 130 (type locality—Mexico, Michoacán, Los Reyes; holotype—USNM 125941).

Oryzomys fulvescens mayensis Goldman, 1918:92 (type locality—Mexico, Campeche, near Yohaltún, Apazote, 200 ft; holotype—USNM 107979).

Oryzomys fulvescens engraciae Osgood, 1945:300 (type locality—Mexico, Tamaulipas, northwest of Ciudad Victoria, Hacienda Santa Engracia, 240 m; holotype—FMNH 54164).

Oryzomys fulvescens pacificus Hooper, 1952: 23 (type locality—Mexico, Chiapas, Mapastepec, 150 ft; holotype—UMMZ 96764).

Remarks.—While we defend our sample sizes and the coarse density of geographic sampling as adequate to clarify the status of *O. vegetus*, they are insufficient to evaluate geographic differentiation within *O. fulvescens* and to address attendant nomenclatural questions to their proper depth. Nevertheless, the several subspecies examined and the morphological divergence encountered warrant some comment on intraspecific variation.

The extensive dispersion of specimens along the second canonical variate principally involves the four subspecific taxa of *O. fulvescens* and suggests a north–south trend of increase in average size, with individuals of *f. fulvescens* and *f. pacificus* smaller, *f. nicaraguae* intermediate, and those of *f. costaricensis* larger (Fig. 7). Although a broad trend may exist (verification with more samples is desirable), individual scores within the conventional subspecies vary greatly and group polygons overlap extensively. Dimensions that load heavily on CV II include IOB, BPL, LM1–3, and WM1, all of which reach their most robust expression in certain samples of *costaricensis*

(for example CR2-3, PA7—Appendix). If one ignores his inclusion of *vegetus* and the later additions of new geographic races, these results provide some corroboration of Goldman's (1918) general remarks on craniodontal variation within *fulvescens*.

Cohesiveness of certain subspecific boundaries, however, is eroded in phenograms generated from clustering of sample means. Whether using a distance or correlation measure of phenetic similarity, OTUs of *f. costaricensis* fail to group exclusively of others representing *fulvescens* proper, *f. pacificus*, and some *f. nicaraguae* (Fig. 8). Certain samples of *f. costaricensis* from central Panama (PA1-3) actually link with northern subspecies instead of geographically proximate OTUs from western Panama (PA7) and eastern Costa Rica (CR2-3). Pygmy rice rats from northern and central Nicaragua (NI1 = *f. nicaraguae*) consistently formed a pair-group with *fulvescens* from Veracruz, a resemblance in accord with the opinion of Jones and Engstrom (1986), who suggested that *nicaraguae* may prove inseparable from the nominate race.

The most divergent OTU (NI2) among our samples of *O. fulvescens* is that drawn from scattered localities along the Pacific coastal region of Nicaragua. Jones & Engstrom (1986) noted the smaller cranial size and pale buff venter of *fulvescens* from this region as compared to those from the central and northern highlands; they assigned, with reservation, the former to *f. costaricensis* and the latter to *f. nicaraguae*. We do not attach much significance to the apparent size divergence of this one OTU in view of its small sample size ($n = 7$), the skewed age representation (mostly young-, some full-, and no old-adults), and the coarse lumping of localities within Nicaragua necessarily employed by us and by Jones & Engstrom (1986). In particular, the reputedly smaller cranial size can be attributed to youthful age representation in this one sample; it is significant that the length of the molar rows,

which once erupted do not increase with age, of the two Nicaraguan OTUs are essentially identical (\bar{X} LM1-3 = 2.86 and 2.87 mm in NI1 and NI2, respectively). Chromatic distinctions of the coastal specimens (paler dorsum and a white to light buff venter) do set them apart from north-central populations (darker dorsal tone and gray venter), and instead resemble examples of *costaricensis* from Costa Rica. As noted by Jones & Engstrom (1986), the geographic extent of this Pacific lowlands morphotype, its possible intergradation with Hooper's (1952) *pacificus* to the north and with Allen's (1893) *costaricensis* to the south, deserves amplification.

Two chromosomal morphologies have been reported, both as *Oryzomys fulvescens*, for populations of *Oligoryzomys* from Central America. Gardner & Patton (1976) described a diploid complement consisting of one large and four small pairs of metacentrics, three pairs of large subtelocentrics, and 18 pairs of small acrocentrics ($2N = 54$; $FN = 68$) for a single individual from near Santa Ana, San José, Costa Rica. In contrast, Haiduk et al. (1979) discovered a higher diploid count (three additional acrocentric pairs; $2N = 60$; $FN = 74$) for three individuals collected northeast of Catemaco, Veracruz, Mexico; they did not attach any taxonomic import to the difference. We have examined the former specimen (LSU 13169) and found it to be a typical example of *O. fulvescens costaricensis*. In view of their origin from Veracruz, and having encountered no other form of *Oligoryzomys* in the region, we presume the latter to represent *O. f. fulvescens*. Taxonomic implication of the reported chromosomal differences, their degree of conservatism, and the existence of still other karyotypic variants within populations now classified as *O. fulvescens* are all topics for future study.

Central American populations and infra-specific taxa of *O. fulvescens*, now divorced of Bangs's (1902) *vegetus* and Goodwin's (1945) *creper* and *reventazoni*, appear con-

specific to us. Yet questions remain—such as the divergence and relationship of populations in western Nicaragua and the significance of the disparate karyotypes reported—and underscore the need for further investigation. The specific limits and systematic standing of forms of *Oligoryzomys* named from South America are far more tentative. Future research should amplify the specimen-based distribution of *fulvescens* south of the Isthmus of Panama and confirm or reject the relationship and synonymy of South American species-group taxa that we have provisionally associated with it (Carleton & Musser 1989, Musser & Carleton 1993). Pending completion of such studies, we below list the Central American specimens examined according to recently published viewpoints on subspecies and their ranges (that is, Hall 1981, Jones & Engstrom 1986).

Oligoryzomys fulvescens costaricensis
(Allen)

Specimens examined.—311, as follows.

Costa Rica: Provincia de Alajuela, Lajas Villa Quesada (AMNH 139735); 5 mi SW San Ramón (KU 71300); Upala, Colonia Puntarenas, Route 4—KM 93, Río Chimirria, 80 m (KU 142726–8); Upala, San José, 45 m (KU 142729); Upala, Aguas Claras, Colonia Libertad, Finca La Anita (KU 142730). Provincia de Cartago, Agua Caliente (KU 16581–2, 16584–6, 27015–6); Cartago, 4800 ft (KU 16535, 16583; UMMZ 66469, 66472, 66476); 3 km S Cartago, 1400 m (KU 27004); Cervantes (AMNH 123501; FMNH 35196–7; MCZ 27805; USNM 250374–5, 256479); La Carpintera (AMNH 9565/7907); Girara (KU 16580); El Guarco (KU 165789, 16588); El Muñeco, 10 mi S Cartago, Río Navarro, 3700 and 3800 ft (UMMZ 67311, 67314); near Paraiso (UMMZ 105658); 1 mi W Paraiso, 1415 m (UMMZ 112286); Santa Teresa, Peralta (AMNH 140364–5, 141890, 141892); 3 mi SE Turrialba, Instituto Interamericano, 602

m (UMMZ 111976–81, 112285); 5 km SE Turrialba (KU 27005–14). Provincia de Guanacaste, 2 km SE (via rd to Caño Negro) Arenal (UMMZ 115513); Finca Jiménez, 0.5 mi E headquarters, 30 m (UMMZ 115291); Cerros de San Juan, 8 mi S Santa Cruz, 1200 ft (UMMZ 65048); Hacienda Santa María, 3200 ft (UMMZ 65218–9); Palo Verde, 2 km S and 12 km E Bolsón, 50 m (KU 143733); Rincón de La Vieja National Park, near headquarters, 780 m (KU 143748). Provincia de Puntarenas, Boruca (AMNH 9572, 9573/7914, 9574/7915, 9575/7916, 9577/7918, 9580/7921; FMNH 5369); Buenos Aires (AMNH 9578/7919, 9579/7920); Cañas Gordas (AMNH 142440–58, 142490–5, 142500); Osa Peninsula, Corcovado National Park, Sirena Station (USNM 565820–1); El General, 2000 and 2150 ft (AMNH 9568/7910, 9581–2/7922–3; UMMZ 66470–1, 66475); Finca Helechales, 910 m (USNM 547947–9); Palmar Sur, 15 m (KU 88240–4); 4 km S San Vito de Java, Finca Las Cruces, 1250 m (UMMZ 116909–10); Monteverde, Pension Quetzal, 1400 m (FMNH 128494). Provincia de San José, Escazú, 3000 ft (AMNH 131738); Monterrey, 22 km S San José, 1000 m (KU 60485), 1100 m (KU 39253, 60486); San Gerónimo de Pirrís (AMNH 123538–9, 123541; FMNH 35198–9; MCZ 27801, 27803–4, 28864–5; USNM 250377, 250380–93, 256480–1); 9.3 mi W (via rd to Dominical) San Isidro del General (UMMZ 105656); 2 km NW Santa Ana (LSUMZ 13169); Sabanilla de Pirrís (USNM 256449). Costa Rica, locality unknown (AMNH 10101, 10103, 19230).

Nicaragua: Carazo, 3 mi NNW Diriamba (KU 71294–9); 3 km N and 4 km W Diriamba, 600 m (KU 110465, 115438). Chinandega, 1 km N Cosiguina, El Paraiso, 20 m (KU 115432). Granada, 10 km SE Guanacaste, Finca El Progreso, 1000 m (KU 106551–2).

Panama: Canal Zone, Albrook Field (USNM 302684); Barro Colorado Island (UMMZ 59935–6; USNM 256183–5); Cu-

rundu (USNM 297943, 301594); Fort Clayton (USNM 297942); Fort Kobbe (USNM 300351); Buena Vista Peninsula, 1.75 km NNW Frijoles (USNM 503718); Rodman Naval Station (USNM 457327–9, 457917). Provincia de Chiriquí, Boquete, 3800, 4000, and 4800 ft (MCZ 10293–4, 10296, 10299, 10307); Río Chebo (ANSP 18386–7, 18511–3, 18515, 18518–20, 18941–2, 19077–8); Colorado Camp, 24 km NNE San Felix, 1275–1325 m (USNM 541162–71, 541173–83); Río Gariche, 5350 ft (ANSP 18408); 7 km NE El Hato de Volcán, 1820 m (UMMZ 117099); Finca Lerida (ANSP 20762, 20769, 20924–5); Finca Santa Clara, 14.5 km NW El Hato del Volcán, 1200–1500 m (USNM 396541–5, 396548–50, 516741, 516743–4, 516746–51, 516754–6, 516760, 516762, 516765, 516768–73, 537619); Río Santa Clara, 4150 ft (ANSP 18383–4, 18627, 18629–33, 18635). Provincia de Coclé, El Valle (USNM 303417–20, 304766). Provincia de Panamá, Cerro Azul, 930 m (USNM 303262, 305676–94, 305697–8, 306951); Cerro Campana (USNM 303416); La Chorrera (AMNH 31431); 6 mi E El Valle (USNM 304767–92); 4 mi E and 1 mi S Pacora (USNM 305675); Panama City, Río Chilibrillo (AMNH 36722–3).

Oligoryzomys fulvescens fulvescens
(Saussure)

Specimens examined.—103, as follows.

Mexico: Estado de Veracruz, Achotal (FMNH 14105–8, 15882); Cerro Azul, 350 ft (KU 30559); Boca del Río, 10 ft (KU 30570); 3 km W Boca del Río, 10 ft (KU 24124–6); Cautlapan, 4000 ft (KU 30573–5); Coscomatepec, 5000 ft (KU 30571–2); Jalapa, 4400 ft (AMNH 12536/10846–12541/10851, 12543/10853–12549/10859, 12583–5; FMNH 5370; USNM 93369–73, 93394); 5 km N Jalapa, 4500 ft (KU 19394); Jico, 6000 ft (FMNH 13112; USNM 55032–3); 2 km W Jico, 4200 ft (KU 19722–3); 20 km E Jesus Carranza, 300 ft (KU 24133–4); 25 km ESE Jesus Carranza, 200 ft (KU 32156); 0.5–3 mi NE Las Minas, 1200–1400

m (USNM 329805–8); Mirador, 3500 ft (KU 24122; USNM 10107/12174); Monte Blanco, 1300 m (KU 29495–6); 2 km N Motorongo, 1500 ft (KU 19400); Orizaba, 4000 ft (USNM 58243–4, 58246–8, 58254–6, 58259–62, 58288), 4200 ft (USNM 63685–8); 3 km SE Orizaba, 5500 ft (KU 19721, 19723); Ozulama, 500 ft (KU 30558); 4 km W Paso de San Juan, 250 ft (KU 24123); Planton Sánchez, 800 ft (KU 88700–2); Potrero Viejo, 1700 ft (KU 24127–9, 24170, 30576–9, 32155); San Andreas Tuxtla (USNM 65540); 3 km E San Andreas Tuxtla, 1000 ft (KU 24130–2); 2 km SSW Tenochtitlán, 60 m (UMMZ 116316–8); Teocelo, 4500 ft (KU 30564–9); 12.5 mi N Tihuatlan, 300 ft (KU 88704); 5 km S Tihuatlan, 700 ft (KU 24119); Tlacolula, 60 km WNW Tuxpan (KU 83067); 15 km ENE Tlacotepec, 1500 ft (KU 24120); 4 km W Tlacotepec, 1700 ft (KU 24121).

Oligoryzomys fulvescens nicaraguae (Allen)

Specimens examined.—28, as follows.

Nicaragua: Boaco, 17 km N and 15 km E Santa Rosa, 300 m (KU 110461). Chontales, 1 km N and 2.5 km W Villa Somoza, 330 m (KU 110464). Jinotega, Yali, 860 m (KU 106546, 106549). Matagalpa, 1 km N and 5 km E Esquipulas, La Danta, 760 and 780 m (KU 115433–4); Santa María de Ostuma, 1250 m (KU 106550); Vijagua (AMNH 29543). Nueva Segovia, 1.5 km N and 1 km E Jalapa, 660 m (KU 110455–7); 4.5 km N and 2 km E Jalapa, 680 m (KU 110453–4); 3.5 km S and 2 km W Jalapa, 660 m (KU 110458–9). Rivas, Isla de Ometepe, 4 km S and 1.5 km E Alta Gracia, 40 m (KU 115439). Zelaya, Cara de Mono, 50 m (KU 115435–6); El Recreo, southern side of Río Mico, 25 m (KU 106553–8, 110462–3, 115437; USNM 337770).

Oligoryzomys fulvescens pacificus (Hooper)

Specimens examined.—22, as follows.

Mexico: Estado de Chiapas, Maspastepec, 45 m (UMMZ 96750–66); Pijijiapan,

10 m (UMMZ 96767–9, 96798); Ariaga, 100 m (UMMZ 96770).

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Appendix.—Descriptive statistics for selected cranial and external variables and OTUs of *Oligoryzomys*.

Species and OTU	n	Mean	Range	SD
Total length				
<i>O. fulvescens fulvescens</i>				
FUL	55	178	157–205	11.6
<i>O. fulvescens costaricensis</i>				
PA3	19	197	184–217	8.0
PA7	24	174	149–198	12.2
CR2	21	177	160–196	10.2
CR4	23	173	150–193	10.4
CR5	21	177	154–197	11.2
<i>O. vegetus</i>				
PA4	12	207	185–235	15.1
PA5	28	192	170–213	10.7
PA6	63	211	191–238	12.6
CR1	4	196	179–216	15.3
CR7	15	193	158–214	14.1
Tail length				
<i>O. fulvescens fulvescens</i>				
FUL	55	101	82–116	7.3
<i>O. fulvescens costaricensis</i>				
PA3	19	112	102–125	6.5
PA7	24	99	85–118	7.3
CR2	21	102	92–115	5.7
CR4	23	102	88–112	6.1
CR5	22	99	90–115	5.7
<i>O. vegetus</i>				
PA4	12	119	110–130	6.6
PA5	28	113	97–126	6.3

Appendix.—Continued.

Species and OTU	n	Mean	Range	SD
PA6	63	126	113–142	8.3
CR1	4	113	107–125	8.3
CR7	15	114	94–129	8.5
Hindfoot length				
<i>O. fulvescens fulvescens</i>				
FUL	57	21.4	19–24	1.1
<i>O. fulvescens costaricensis</i>				
PA3	20	22.1	21–23	0.8
PA7	24	20.2	18–23	1.4
CR2	22	20.1	18–21	1.1
CR4	23	19.9	18–21	0.8
CR5	23	20.8	17–23	1.4
<i>O. vegetus</i>				
PA4	13	23.7	20–25	1.3
PA5	30	22.9	21–26	1.0
PA6	62	24.5	23–27	1.0
CR1	11	22.4	21–24	1.1
CR7	16	23.0	20–25	1.4
Occipitonasal length				
<i>O. fulvescens fulvescens</i>				
FUL	50	21.2	19.6–23.7	0.8
<i>O. fulvescens costaricensis</i>				
PA3	20	22.0	21.5–23.0	0.4
PA7	24	21.7	20.2–23.2	0.7
CR2	14	22.0	20.8–23.9	0.9
CR4	16	21.3	19.2–23.0	1.1
CR5	15	21.5	20.1–22.5	0.7
<i>O. vegetus</i>				
PA4	8	23.3	22.3–24.4	0.7
PA5	33	22.5	20.9–24.0	0.7
PA6	49	23.2	21.0–25.6	1.0
CR1	13	22.8	21.1–24.1	0.8
CR7	15	22.4	21.4–23.6	0.7
Zygomatic breadth				
<i>O. fulvescens fulvescens</i>				
FUL	50	11.0	10.3–12.2	0.4
<i>O. fulvescens costaricensis</i>				
PA3	20	11.3	10.8–11.9	0.4
PA7	24	11.0	10.1–11.9	0.4
CR2	14	11.3	10.6–12.4	0.5
CR4	16	11.1	10.0–11.8	0.5
CR5	16	11.2	10.4–11.8	0.4
<i>O. vegetus</i>				
PA4	8	12.3	11.8–12.9	0.4
PA5	33	11.9	10.8–12.9	0.5

Appendix.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
PA6	49	12.0	11.1–13.5	0.5
CR1	13	11.9	11.1–12.5	0.5
CR7	16	11.7	10.8–12.5	0.4
Breadth of braincase				
<i>O. fulvescens fulvescens</i>				
FUL	50	10.0	9.4–10.5	0.3
<i>O. fulvescens costaricensis</i>				
PA3	20	10.0	9.7–10.4	0.2
PA7	24	9.9	9.4–10.4	0.2
CR2	14	10.3	9.9–10.7	0.2
CR4	16	10.1	9.6–10.5	0.3
CR5	16	10.1	9.7–10.4	0.2
<i>O. vegetus</i>				
PA4	8	10.9	10.6–11.2	0.2
PA5	33	10.7	10.1–11.2	0.3
PA6	49	10.7	10.3–11.3	0.2
CR1	13	10.7	10.1–11.0	0.2
CR7	16	10.6	10.3–10.8	0.2
Interorbital breadth				
<i>O. fulvescens fulvescens</i>				
FUL	50	3.4	3.1–3.7	0.1
<i>O. fulvescens costaricensis</i>				
PA3	20	3.7	3.5–3.9	0.1
PA7	24	3.7	3.5–4.2	0.1
CR2	14	3.7	3.4–4.1	0.1
CR4	16	3.7	3.3–3.9	0.1
CR5	16	3.6	3.3–3.9	0.1
<i>O. vegetus</i>				
PA4	8	3.7	3.5–4.0	0.1
PA5	33	3.6	3.1–4.0	0.1
PA6	49	3.6	3.3–3.9	0.1
CR1	13	3.7	3.5–4.0	0.1
CR7	16	3.7	3.4–3.9	0.1
Length of rostrum				
<i>O. fulvescens fulvescens</i>				
FUL	50	6.3	5.5–7.0	0.4
<i>O. fulvescens costaricensis</i>				
PA3	20	6.5	6.0–7.1	0.2
PA7	24	6.4	5.8–7.1	0.3
CR2	14	6.7	6.1–7.6	0.4
CR4	16	6.4	5.3–7.2	0.5
CR5	15	6.4	6.0–7.1	0.3
<i>O. vegetus</i>				
PA4	8	6.9	6.4–7.5	0.3
PA5	33	6.7	5.7–7.4	0.4

Appendix.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
CR1	13	7.0	6.4–7.6	0.3
CR7	15	6.6	6.1–7.1	0.3
Postpalatal length				
<i>O. fulvescens fulvescens</i>				
FUL	50	7.0	6.1–7.9	0.6
<i>O. fulvescens costaricensis</i>				
PA3	20	7.5	7.1–7.9	0.2
PA7	24	7.1	6.5–7.7	0.3
CR2	14	7.2	6.7–8.5	0.5
CR4	13	7.0	6.2–7.9	0.6
CR5	16	7.0	6.4–7.8	0.4
<i>O. vegetus</i>				
PA4	7	7.9	7.5–8.9	0.5
PA5	33	7.4	6.7–8.2	0.4
PA6	49	7.7	6.7–8.5	0.5
CR1	11	7.4	6.8–8.0	0.4
CR7	16	7.3	6.9–7.7	0.2
Length of diastema				
<i>O. fulvescens fulvescens</i>				
FUL	50	5.1	4.2–5.8	0.3
<i>O. fulvescens costaricensis</i>				
PA3	20	5.4	5.1–5.7	0.2
PA7	24	5.1	4.7–5.8	0.3
CR2	14	5.3	4.9–6.3	0.4
CR4	17	5.1	4.3–5.8	0.4
CR5	16	5.2	4.9–5.8	0.3
<i>O. vegetus</i>				
PA4	8	5.7	5.4–6.2	0.3
PA5	33	5.5	4.9–6.2	0.3
PA6	49	5.7	4.9–6.6	0.4
CR1	13	5.7	5.2–6.4	0.4
CR7	16	5.5	5.1–5.9	0.2
Length of incisive foramen				
<i>O. fulvescens fulvescens</i>				
FUL	50	3.7	3.3–4.1	0.3
<i>O. fulvescens costaricensis</i>				
PA3	20	4.0	3.7–4.5	0.2
PA7	24	3.9	3.6–4.3	0.2
CR2	14	4.0	3.7–4.3	0.2
CR4	17	3.7	3.1–4.0	0.2
CR5	16	3.8	3.5–4.2	0.2
<i>O. vegetus</i>				
PA4	8	3.8	3.7–4.1	0.1
PA5	33	3.7	3.1–4.0	0.2

Appendix.—Continued.

Species and OTU	n	Mean	Range	SD
PA6	49	3.7	3.3–4.3	0.2
CR1	13	3.7	3.4–4.0	0.2
CR7	16	3.7	3.3–4.0	0.2
Breadth of bony palate				
<i>O. fulvescens fulvescens</i>				
FUL	50	3.9	3.7–4.2	0.1
<i>O. fulvescens costaricensis</i>				
PA3	20	4.0	3.7–4.2	0.1
PA7	24	3.9	3.6–4.3	0.1
CR2	14	4.0	3.8–4.4	0.1
CR4	17	4.0	3.8–4.2	0.1
CR5	16	4.1	3.8–4.4	0.1
<i>O. vegetus</i>				
PA4	8	4.3	4.2–4.5	0.1
PA5	33	4.2	3.9–4.4	0.1
PA6	49	4.3	4.0–4.8	0.2
CR1	13	4.2	3.9–4.5	0.2
CR7	16	4.0	3.8–4.2	0.1
Breadth of zygomatic plate				
<i>O. fulvescens fulvescens</i>				
FUL	50	1.8	1.4–2.1	0.1
<i>O. fulvescens costaricensis</i>				
PA3	20	2.1	1.9–2.3	0.1
PA7	24	2.0	1.7–2.2	0.1
CR2	14	2.0	1.8–2.2	0.1
CR4	17	1.8	1.5–2.1	0.2
CR5	16	1.9	1.5–2.1	0.1

Appendix.—Continued.

Species and OTU	n	Mean	Range	SD
<i>O. vegetus</i>				
PA4	8	1.9	1.8–2.0	0.1
PA5	33	1.8	1.4–2.2	0.2
PA6	49	1.9	1.5–2.1	0.1
CR1	13	1.9	1.6–2.2	0.1
CR7	16	1.8	1.6–2.0	0.1
Length of maxillary tooththrow				
<i>O. fulvescens fulvescens</i>				
FUL	50	2.8	2.5–3.0	0.10
<i>O. fulvescens costaricensis</i>				
PA3	20	3.0	2.8–3.2	0.10
PA7	24	3.1	2.9–3.2	0.09
CR2	19	3.1	2.8–3.3	0.11
CR4	22	2.9	2.8–3.1	0.08
CR5	24	3.0	2.8–3.1	0.08
<i>O. vegetus</i>				
PA4	12	3.0	2.8–3.1	0.08
PA5	34	2.9	2.8–3.1	0.06
PA6	58	2.9	2.7–3.1	0.08
CR1	13	2.9	2.8–3.1	0.08
CR7	16	2.8	2.6–3.0	0.10

OTU Codes.—FUL: Mexico, Veracruz, various localities; CR1: Costa Rica, Limón, Valle El Silencio; CR2: Costa Rica, Puntarenas, Cañas Gordas; CR4: Costa Rica, San José, San Gerónimo Pirris; CR5: Costa Rica, Cartago, valley of Río Reventazón; CR7: Costa Rica, Puntarenas, Monteverde; PA3: Panama, Chiriquí, Colorado Camp; PA4: Panama, Chiriquí, Boquete; PA5: Panama, Chiriquí, Cerro Punta & vicinity; PA6: Panama, Chiriquí, Siola; PA7: Panama, Chiriquí, Finca Santa Clara.